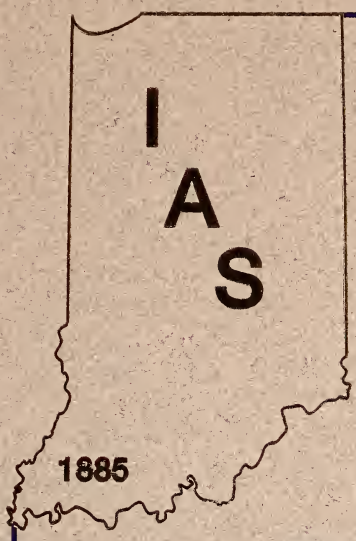

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FIFTEEN YEARS OF FOREST SUCCESSION IN HAPPY VALLEY, JEFFERSON COUNTY, INDIANA

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ABSTRACT: In April 1974, a major tornado severely damaged the forest in Happy Valley, Jefferson County, Indiana. The pre-tornado forest was a sugar maple-Ohio buckeye community. In the fall of 1974, the forest was sampled on three transects across the valley. Virtually all the canopy trees had been removed or damaged; the dominant species (dbh ≥ 5 cm) in the most disturbed part of the forest were sugar maple, white oak spp., and white ash. Seven years later, the forest was sampled along the same three transects and described as a sugar maple-elm spp.-Ohio buckeye-redbud community. Fifteen years after the tornado (this study), the forest was sampled along the same transects and found to be a sugar maple-slippery elm community. Of secondary importance in the more severely damaged northern portion of the valley were sycamore and black maple on the valley floor and basswood, hackberry, and species of the white oak section of *Quercus* on the slopes. Of secondary importance in the less damaged southern portion of the valley were black walnut and box elder on the valley floor and white ash and northern red oak on the slopes. Predictions of change in forest structure and composition are discussed relative to the recent history of forest recovery.

KEYWORDS: *Acer saccharum, Aesculus glabra,* forest composition, forest structure, *Fraxinus americana,* Jefferson County, Indiana, mixed mesophytic forest, *Quercus* spp., *Ulmus rubra.*

INTRODUCTION

On 3 April 1974, a major tornado blew through the town of Hanover in southeastern Indiana, traversing the Hanover College campus and the adjacent wooded Happy Valley rendering extensive damage to both. In the fall of 1974, Bailey and MacMillan (1977) censused the standing live trees (dbh ≥ 5 cm) which remained. They found that the storm had reduced the tree population by as much as one-third. With virtually all canopy trees removed and a large portion of the forest floor exposed, Happy Valley became a natural laboratory for studying secondary succession.

Analysis of pre-tornado data (collected at different times by J. Dan Webster and J. Davis) suggested that the original valley forest was a sub-climax sugar maple-Ohio buckeye (*Acer saccharum-Aesculus glabra*) community. Following the tornado, Bailey and MacMillan (1977) described the remaining forest as a sugar maple-white ash-white oak spp. (*A. saccharum-Fraxinus americana-Quercus* spp.) community. In 1981, Martin and MacMillan (1982) recensused the val-

ley forest and found that sugar maple, elm (*Ulmus*) spp., Ohio buckeye, and redbud (*Cercis canadensis*) were dominant in the most severely damaged (northern) part of the valley, whereas sugar maple, white ash, and white oak spp. remained dominant in the less disturbed (southern) portion of the valley.

The objectives of the present study were to (1) catalog the current structure and composition of the Happy Valley forest, (2) compare the changes that had occurred in the forest community over the last fifteen years, and (3) suggest what further changes might occur in community structure in the valley forest in the future.

STUDY SITE

Happy Valley is located at 38° 43′ N and 85° 27′ W in the Muscatatuck Flats and Canyons Section of the Bluegrass Natural Region of southeastern Indiana (Homoya, *et al.*, 1985) adjacent to Hanover College, Jefferson County, Indiana. The valley runs approximately northwest to southeast and is an area of rather sharp relief. From the flat Avonburg, Rossmoyne, and Ryker silt loam soils (0 to 6% slopes) that surround the valley, the wooded slopes with Eden-Caneyville complex soils (25 to 60% slopes) descend 75 m to a narrow valley floor with Dearborn channery silt loam soils (Nickell, 1985). An intermittent stream that drains upland agricultural fields and woodlands flows through the valley and empties into the Ohio River. The full width of the valley and approximately two-thirds of its total length were included in this study. Three line transects were followed across the valley: transects 1 (north) and 2 (mid) lie within the windthrow area and transect 3 (south) lies south of the most damaged area (Figure 1). These were the same transects laid out by Bailey and MacMillan in 1974 and followed by Martin and MacMillan in 1981.

METHODS

The point-centered-quarter method described by Cottam and Curtis (1956) was used to sample the tree population, using sampling intervals of 15 m. The field data collected included distance along the transect, point-to-tree distance, diameter at breast height (dbh), species, and comments or observations. Nomenclature follows that of Gleason and Cronquist (1991).

Transect 1 was 345 m long and included 95 stems; transect 2 was 405 m long and included 109 stems; and transect 3 was 390 m long and included 103 stems. The data were analyzed using the methods of Cox (1990) to estimate mean point-to-tree distance, mean area per tree, and total density of trees (number of trees/hectare). Relative density, relative frequency, and relative dominance (i.e., basal area) were calculated and then summed to yield the importance value by species.

Data from transects 1 and 2 were combined to provide more complete information about the damaged area; this area is referred to as the "damaged woods." Martin and MacMillan (1981) referred to the same area as the "woods." Data

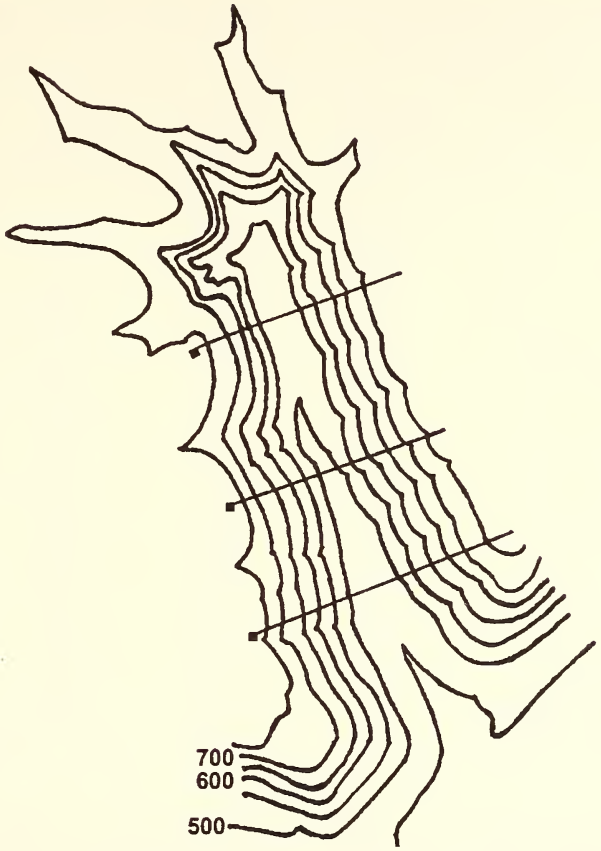

Figure 1. A map of Happy Valley, Jefferson County, Indiana, showing the location of the three transects discussed in the text. Transect 1 is at the top of the map, and transect 3 is at the bottom.

from the relatively less damaged area (transect 3 at the south end of the valley) was used for comparison.

Comparisons of the vegetative communities sampled on the three transects were made using Sorenson's quotient of similarity (Brower, *et al.*, 1990) and the Bray and Curtis (1957) similarity index as measures of community similarity. Sorenson's quotient of similarity is calculated as:

$$CC_S = 2C/(s_1 + s_2)$$

where C is the number of species common to both sites, s_1 is the number of species at site 1, and s_2 is the number of species at site 2. The Bray and Curtis similarity index is calculated as:

$$CC_B = (2W/(a + b))100$$

where W is the sum of the lower importance values for those species which are common to both sites, a is the sum of the importance values for all the species at site 1, and b is the sum of the importance values for all the species as site 2.

Table 1. The characteristics of the Happy Valley forest along transect 1 (north end of the valley) fifteen years after the tornado.

Species	Relative Density	Relative Frequency	Relative Dominance	Importance Value
Ulmus rubra	33.33	19.66	29.78	82.77
Acer saccharum	22.92	21.31	22.10	66.33
Tilia americana	9.38	13.11	3.05	25.54
Acer nigrum	8.33	11.48	3.69	23.50
Platanus occidentalis	1.04	1.64	15.43	18.11
Cercis canadensis	8.33	8.20	1.46	17.99
Quercus rubra	1.04	1.64	10.40	13.08
Quercus michauxii	3.12	4.92	3.55	11.59
Aesculus glabra	2.08	3.28	3.60	8.97
Celtis occidentalis	3.12	3.28	1.62	8.02
Paulownia tomentosa	2.08	3.28	2.48	7.84
Carya cordiformis	1.04	1.64	2.15	4.83
Liriodendron tulipifera	1.04	1.64	0.31	2.99
Juglans nigra	1.04	1.64	0.19	2.87
Ostrya virginiana	1.04	1.64	0.10	2.78
Fraxinus quadrangulata	1.04	1.64	0.09	2.77

RESULTS

Composition of the Forest After 15 Years. Slippery elm and sugar maple were dominant on transect 1 (importance values = 83 and 66, respectively), based on their relative density, frequency, and dominance (Table 1). These two species were followed by basswood (*Tilia americana*) on the mesic east-facing slope and black maple (*Acer nigrum*) on the valley floor (importance values = 26 and 24, respectively). For basswood and black maple, their large relative frequency but not their basal area significally influenced their importance values. Redbud was relatively abundant on the drier west-facing slope, but its small basal area kept its importance value (18) low. On the other hand, one large sycamore (*Platanus occidentalis*), its top damaged but its trunk still intact, and one large red oak (*Quercus rubra*) had importance values of 18 and 13, respectively. These values were nearly equal to those of the more numerous redbud. Nine other species had lower importance values.

On transect 2 (Table 2), sugar maple was clearly the dominant species (importance value = 91) followed by slippery elm (importance value = 54). These two species were important in all three relative measures. Slippery elm was abundant across the valley, whereas sycamore (importance value = 30) and boxelder (*Acer negundo*; importance value = 10) tended to replace sugar maple near the creek bed, while chinquapin oak (*Quercus muehlenbergii*; importance value = 26) was more abundant on the west-facing slope. Hackberry (*Celtis occiden-*

Table 2. The characteristics of the Happy Valley forest along transect 2 (middle portion of the valley) fifteen years after the tornado.

Species	Relative Density	Relative Frequency	Relative Dominance	Importance Value
Acer saccharum	38.53	27.79	24.52	90.84
Ulmus rubra	22.02	20.84	10.68	53.54
Platanus occidentalis	2.75	2.78	24.91	30.44
Quercus muehlenbergii	6.42	6.95	12.14	25.51
Celtis occidentalis	4.59	6.95	2.36	13.90
Fraxinus americana	2.75	4.17	6.72	13.64
Aesculus glabra	3.67	4.17	3.13	10.97
Acer negundo	4.59	4.17	0.86	9.62
Quercus michauxii	1.83	2.78	4.59	9.20
Acer nigrum	2.75	4.17	0.74	7.66
Prunus serotina	2.75	4.17	0.50	7.42
Ostrya virginiana	2.75	4.17	0.47	7.39
Quercus rubra	0.92	1.39	4.05	6.36
Juglans nigra	0.92	1.39	2.98	5.29
Catalpa speciosa	0.92	1.39	1.13	3.44
Gymnocladus dioica	0.92	1.39	0.14	2.45
Quercus velutina	0.92	1.39	0.08	2.39

talis), white ash, and Ohio buckeye had importance values of 14, 14, and 11, respectively. Nine other species had lower importance values.

At the southern end of the valley, sugar maple was dominant (importance value = 73), although it was nearly replaced by black walnut (*Juglans nigra*; importance value = 34) and box elder (importance value = 21) on the valley floor (Table 3). Slippery elm was again second in importance (importance value = 43) due to both frequency and basal area. White ash, red oak, and black maple (importance values = 28, 21, and 18, respectively) had moderate importance values. Seven other species had lower importance values.

Data from the most damaged area of the valley (transects 1 and 2) were combined in Table 4 for comparison with the less-damaged transect 3 and with previous studies of the Happy Valley forest. In the damaged woods data (Table 4), sugar maple (importance value = 80) and slippery elm (importance value = 65) were dominant due to their high density, frequency, and dominance (i.e., basal area). Sycamore and chinquapin oak had moderate importance values (importance values = 26 and 15, respectively) based on their relative dominance. Black maple (importance value = 15) was next due to its frequency; basswood, hackberry, swamp chestnut oak (*Quercus michauxii*), and Ohio buckeye (importance values = 12, 11, 10, and 10, respectively) had intermediate importance values. Fourteen other species had lower importance values.

Table 3. The characteristics of the Happy Valley forest along transect 3 (southern portion of the valley) fifteen years after the tornado.

Species	Relative Density	Relative Frequency	Relative Dominance	Importance Value
Acer saccharum	32.04	23.08	18.15	73.27
Ulmus rubra	8.74	12.31	21.50	42.55
Juglans nigra	7.77	7.69	18.18	33.64
Fraxinus americana	10.68	9.23	8.47	28.38
Quercus rubra	3.88	4.62	12.30	20.80
Acer negundo	8.74	6.15	5.67	20.56
Acer nigrum	5.82	7.69	4.65	18.16
Maclura pomifera	3.88	4.62	6.18	14.68
Aesculus glabra	4.85	7.69	1.22	13.76
Cercis canadensis	4.85	4.62	1.53	10.99
Quercus michauxii	3.88	4.62	1.49	9.99
Celtis occidentalis	1.94	3.08	0.46	5.48
Asimina triloba	1.94	3.08	0.10	5.12
Carpinus caroliniana	0.97	1.54	0.09	2.60

Values of Sorenson's quotient of similarity (Brower, *et al.,* 1990) for these three transects ranged from 0.468 to 0.645 (Table 5). For the Bray and Curtis (1957) similarity index, the values ranged from 59.48 to 64.72.

Structure of the Forest After 15 Years. The mean point-to-tree distance in the damaged woods region of the valley (transects 1 and 2) decreased by 33% in seven years and by 41% in 15 years (Table 6). In the less disturbed region of the valley (transect 3), the mean distance decreased by 5% in seven years (1974 to 1981) and by 13% in 15 years. Mean tree density increased by 117% in 7 years and by 178% in 15 years in the most disturbed area; in the less disturbed area, density increased by 17% in 7 years and by 37% in 15 years.

DISCUSSION

Damaged Woods Data Compared Over 15 Years. When data from 1974, 1981, and 1989 are compared, the importance value of the dominant sugar maple is seen to decrease from 122 in 1974, to 82 in 1981, and to 80 in 1989; this represents a 34% decease in importance. At the same time, the importance value of fast-growing slippery elm increased from 17 in 1974, to 34 in 1981, and to 65 in 1989; this represents an increase of 276% in importance. The sugar maples must have been understory trees in 1974; then, when the canopy was destroyed, they were released and grew rapidly. After 15 years, their relative density and frequency had diminished due to the more rapid proliferation of other species such as slippery elm. If these trends continue, slippery elm will soon be the dominant tree in this most-damaged portion of the valley.

Table 4. A summary of the data from the most severely damaged portion (transects 1 and 2 combined) of the Happy Valley forest fifteen years after the tornado.

Species	Relative Density	Relative Frequency	Relative Dominance	Importance Value
Acer saccharum	31.22	24.81	23.64	79.67
Ulmus rubra	27.32	20.30	17.60	65.22
Platanus occidentalis	1.95	2.26	21.47	25.68
Quercus muehlenbergii	3.41	3.76	7.73	14.90
Acer nigrum	5.36	7.52	1.81	14.69
Tilia americana	4.39	6.02	1.11	11.52
Celtis occidentalis	3.90	5.26	2.09	11.25
Quercus michauxii	2.44	3.76	4.21	10.41
Aesculus glabra	2.93	3.76	3.30	9.99
Quercus rubra	0.98	1.50	6.35	8.83
Cercis canadensis	3.90	3.76	0.53	8.19
Fraxinus americana	1.46	2.26	4.28	8.00
Acer negundo	2.44	2.26	0.55	5.25
Ostrya virginiana	1.95	3.01	0.34	5.30
Juglans nigra	0.98	1.50	1.97	4.45
Prunus serotina	1.46	2.26	0.32	4.04
Paulownia tomentosa	0.98	1.50	0.90	3.38
Carya cordiformis	0.49	0.75	0.78	2.02
Catalpa speciosa	0.49	0.75	0.72	1.96
Liriodendron tulipifera	0.49	0.75	0.11	1.35
Gymnocladus dioica	0.49	0.75	0.09	1.33
Quercus velutina	0.49	0.75	0.05	1.29
Fraxinus quadrangulata	0.49	0.75	0.03	1.27

Large boles of several species survived the tornado but then declined in importance later. One possible explanation for this pattern is that the tops of the trees were damaged by the cyclonic winds, opening the boles for infection. When the trees were censused after the tornado in the fall of 1974, the boles were still intact, and they contributed to the overall importance value of the species. However, after 7 and 15 years, the damaged and infected boles had died or fallen and were not counted. This pattern is illustrated by the change in importance value and rank order of white ash, whose importance value changed from 21, to 5, and then to 8 and, whose rank changed from second, to fifteenth, and then to twelfth in 1974, 1981, and 1989, respectively. Black walnut's importance value and rank also reflect this pattern; its importance value changed from 14, to 1, and then to 4, and its rank from seventh, to twenty-first, and then to fifteenth in 1974, 1981, and 1989, respectively. White ash is predicted to increase in importance over the next 5 to 10 years as the large seedling population in the valley grows into the sapling stage. The importance value of slow-growing black walnut is expected to decrease over the next several years until the canopy closes.

Table 5. A comparison of similarity between transects using Sorenson's quotient of similarity (Brower, *et al.*, 1990) and the Bray and Curtis (1957) similarity index as measures of community similarity.

Paired Transects	Community Similarity	
	Sorenson	Bray and Curtis
1 & 2	0.606	61.28
1 & 3	0.600	59.48
2 & 3	0.645	61.34
1 + 2 & 3	0.468	64.72

Sycamore exhibited a different pattern. Many sycamore on the valley floor were windthrown by the tornado. However, a few large boles still remained upright after 15 years, and their damaged tops were bushy with small branches. Sycamore's importance value changed from 18, to 14, and then to 26, and its rank from fourth, to eighth, and then to third in 1974, 1981, and 1989, respectively. This pattern of change is due almost entirely to the persistent large trees that add greatly to the relative dominance compared to the dynamic changes of the many small stems of most other species growing on the valley floor. The importance of sycamore in the valley is predicted to decrease as the large old stems die and as other species increase in basal area. However, a second factor may complicate this picture. Some fallen sycamore boles with adequate root systems have live branches that are very tree-like in height and diameter. Whether or not these trees-from-logs will continue to survive is hard to predict.

Basswood, an infrequent subcanopy tree on the mesic east-facing slope and valley floor, forms coppices. Thus, its relative density and relative frequency values are moderate, but its relative dominance value is small. Its importance value changed from 4, to 14, and finally to 12, and its rank from thirteenth, to seventh, and then to sixth in 1974, 1981, and 1989, respectively. Basswood's relative density and relative frequency should decease and its relative dominance should increase as one of the multiple stems in each coppice becomes stronger and larger.

The importance value for redbud was 4, 17, and 8, and its rank was fifteenth, fourth, and eleventh in 1974, 1981, and 1989, respectively. This variation is due mostly to changes in its relative density and relative frequency. The apparent fluctuation in importance value might be due to relatively rapid growth and a short lifespan. In this case, continued oscillation of redbud's importance value is expected in the future. Another possibility is that redbud would show rapid growth when the canopy was destroyed and then die as the canopy closed. In this case, redbud's importance value will remain low.

The importance value of Ohio buckeye went from 15, to 35, and then to 10, and its rank went from sixth, to second, and then to ninth in 1974, 1981, and 1989, respectively. This pattern was due to the abundance of moderate-diam-

Table 6. Changes in Happy Valley forest structure over the fifteen years following the tornado of 1974.

Year	Transect Number	Mean Point-To-Tree Distance (m)	Mean Area/Tree (m^2)	Density (trees/ha)
1973[a]	Pre-tornado	4.4	19.5	512
1974[b]	Mean of 1 + 2	4.9	23.6	426[d]
	3	3.9	15.2	625
1981[c]	Mean of 1 + 2	3.3	11.0	926[d]
	3	3.7	13.7	730
1989[e]	Mean of 1 + 2	2.9	8.5	1186[d]
	3	3.4	11.7	857

[a] J. Davis, unpubl. data.
[b] Bailey and MacMillan, 1977.
[c] Martin and MacMillan, 1982.
[d] The mean data from transects 1 and 2 represent the more damaged area of the valley.
[e] Present data.

eter buckeye stems that had their tops blown off in the tornado. These stems branched rapidly at the top, persisted for a few years, and contributed to the large importance value in 1981. However, the stems had become infected, died, and fallen by 1989. The importance value of shade-tolerant Ohio buckeye is predicted to increase once the canopy closes.

The importance value of hackberry has changed little in the last 15 years; its importance value was 10, 11, and 11, and its rank was tenth, tenth, and seventh in 1974, 1981, and 1989, respectively. This stability appears to be due to its abundance and rapid growth. Hackberry's importance value is predicted to remain stable over the next several years.

Oaks have been a minor component of the damaged woods in Happy Valley since the tornado. However, their specific identification has been difficult. What Bailey and MacMillan (1975) identified as *Quercus bicolor* (swamp white oak) is now identified as *Q. michauxii* (swamp chestnut oak), and what they identified as *Q. borealis* is now correctly named *Q. rubra* (northern red oak). For that reason, and because of the difficulty in identifying oak saplings, Martin and MacMillan (1982) grouped them into the red oaks and white oaks.

Tulip (or yellow) poplar (*Liriodendron tulipifera*), an invader species of disturbed sites, was not found in the disturbed woods in 1974, but the species had an importance value of 2 in 1981 and 1 in 1989; it ranked nineteenth and twentieth in 1981 and 1989, respectively. The importance value of this fast-growing species is predicted to increase over the next 5 years.

Community Similarity. Sorenson's quotient of similarity and the Bray and Curtis similarity index were used to compare the plant communities sampled on the three transects across Happy Valley (Table 5). In all comparisons between transects, community similarity values were less than 65%, indicating quite dissimilar communities. Even the comparison between transects 1 and 2, which represent that portion of the valley most damaged in the 1974 tornado, shows dissimilar composition. This difference is also seen in the species found on transects 1 and 2 (Tables 1 and 2). Unfortunately, no record of the pre-tornado composition of the northern end of the valley exists for comparison.

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EFFECTS OF MIXED FERTILIZER LEVELS AND HARVEST INTERVALS ON THE YIELD AND MINERAL CONCENTRATION OF THE FLUTED PUMPKIN, *TELFAIRIA OCCIDENTALIS* HOOK.

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ABSTRACT: Fluted pumpkin is a viny vegetable crop whose leaves and seeds are commonly cooked and eaten by humans in eastern Nigeria. The plant is also a palatable leafy feed for goats, as owners of unfenced fluted pumpkin gardens often learn. The leaf of the vegetable is eaten mainly for carbohydrate and protein, whereas the seeds are eaten mainly for carbohydrate, oil, and vitamins. Experiments were conducted in Port Harcourt, Nigeria, to evaluate the effects of mixed fertilizer (15-15-15) levels and harvest intervals on the yield and mineral concentration of fluted pumpkin. The results showed that harvests at 2-weekly intervals gave significantly ($P = 0.05$) higher yields than harvests at 4-weekly intervals. Increases in fertilizer levels had no significant effect on total fresh weight yield. However, as fertilizer levels increased, the leaves were greener and more attractive; higher concentrations of N, P, and K in the leaf blades were obtained from the 2-weekly harvests rather than the 4-weekly harvests. These results suggest that for increased yield of leaves and vines and for tender, fresher, and more nutritious leaves, the fluted pumpkin should be harvested every two weeks. Farmers who grow the fluted pumpkin in the dry season should fertilize the crop at the moderate rate of 200 kg/ha of 15-15-15 (as $N\text{-}P_2O_5\text{-}K_2O$) and adopt the practice of a 2-weekly harvest interval.

KEYWORDS: Fertilizer response, fluted pumpkin, harvest interval, mineral concentration, *Telfairia occidentalis* Hook., yield.

INTRODUCTION

The study of the interaction between fertilizer level and harvest interval has received considerable research attention, especially in crops such as cowpea (*Vigna unguiculata*; Godfrey-Sam-Aggrey, 1973), onion (*Allium cepa*; Hassan and Ayoub, 1978), alfalfa (*Medicago sativa*; Ossom, *et al.*, 1983), and rye (*Secale*

cereale; Shim, 1976). Only a few such studies have been conducted on the fluted pumpkin (*Telfairia occidentalis* Hook.). In eastern Nigeria, despite the widespread cultivation of the crop, little attention has been paid to how fertilization and harvest frequency affect its yield. Ossom (1986) established that 2-weekly harvests gave significantly higher total dry matter yield than 6- and 8-weekly harvests. Nangju (1976) reported that decreasing harvest intervals reduced cowpea seed yield. Workers at the International Institute of Tropical Agriculture (1972) observed that fertilizer rates had no significant effect on total yield and yield of the edible portion of jute (*Corchorus olitorius*); they also reported that fertilizer levels had no significant effect on yield of swamp cabbage (*Ipomoea reptans*). Application of fertilizers is known to increase the quality and mineral concentration in most crops (Cochran, *et al.*, 1978; Hageman, *et al.*, 1978; Mathias, *et al.*, 1978; and Ossom, *et al.*, 1991). For the fluted pumpkin, more information is required on the effect of fertilizers on the concentration of minerals in the plant's leaves and stems as a first step to improving the nutrient quality of this vegetable crop.

Farmers who cultivate the fluted pumpkin in Nigeria do not use any specific harvest interval or fertilizer level; they harvest the crop as the need arises. Little or no artificial fertilizer is applied. The present study was aimed at gaining information on the influence of different fertilizer levels and harvest intervals on the yield and mineral concentration of the leaves and vines of the fluted pumpkin to enable husbandry and management recommendations to be made to local farmers.

MATERIALS AND METHODS

The experiment was conducted in the dry season from December 1988 to June 1989 at the Teaching and Research Farm of the University of Science and Technology, Port Harcourt, that lies on latitude 4°46′ N and longitude 7° 01′ E, with a mean annual rainfall of 2,000 mm (Food and Agricultural Organization, 1984). The soil, a Typic Paleudult (sandy loam), contained at 0-15 cm depth 0.09 percent total N (determined by the semi-micro Kjeldahl Method), 20.18 ppm available P (determined by Bray and Kurtz No. 1 Method), and 42.50 ppm exchangeable K (determined by flame photometry) and had a pH of 4.6. The land was plowed and harrowed before planting. The factorial experiment with 3 fertilizer (15-15-15) levels of 0, 200, and 400 kg/ha (Ethirveerasingam, *et al.*, 1985) and 2 harvest intervals at 2 and 4 weeks (Ossom, 1986) was arranged in a randomized complete block design. Each of the 6 treatments was replicated 4 times; plot measurements were 5 m by 5 m.

Crop Establishment and Maintenance. Three pre-sprouted seedlings were planted at a spacing of 1.5 m by 1.5 m giving 13,333 plants/ha (Cochran, *et al.*, 1978). Four weeks after planting, a mixed fertilizer (15-15-15 as N-P_2O_5-K_2O) was ring-applied around each stand at rates of 0, 200, and 400 kg/ha after weeding. Weeds were controlled by hoeing at 4 weeks after planting and, thereafter, every 6 weeks.

Table 1. The distribution of rainfall during the period of this experiment.

Date	Rainfall (mm)	Irrigation (mm)	No. of Days With up to 0.1 mm	Total Water Use (mm)
Dec. 1988	30.2	5.1	4	35.3
Jan. 1989	0.0	20.6	4	20.6
Feb. 1989	0.0	20.6	4	20.6
Mar. 1989	117.3	0.0	11	117.3
Apr. 1989	191.1	0.0	11	191.1
May 1989	124.3	0.0	13	124.3
June 1989	173.4	0.0	16	173.4

Watering. Watering was done at the rate of 2.57 mm irrigation/week for the first 2 weeks after planting and increased to 5.14 mm/week from 3-9 weeks after planting. Watering was discontinued at 10 weeks after planting, when the first heavy rain occurred. Table 1 shows the monthly rainfall and irrigation distribution during the period of the experiment.

Harvesting and Mineral Analysis. The first harvest was taken at 8 weeks after planting; subsequent harvests were at the specified intervals until 24 weeks after planting. At harvest, each vine was cut off at a node about 50 cm from the growing tip, and the total fresh weight/plot of harvested leaves and vines was recorded. Sub-samples of 300 g/plot were collected from the weighed samples and separated into leaf blades, petioles, and vines; these samples were weighed separately, bagged, and dried to constant weight in a ventilated hot-air oven at 80° C for 7 days. The dried leaf blade samples were ground using a micro-hammer mill and sieved through a 0.025 mm mesh screen. N, P, and K analyses were carried out on the samples at 8, 10, 20, 22, and 24 weeks after planting. N was determined by the conventional micro-Kjeldahl Method; P was assessed after dry ashing by the vanadomolybdate method with absorption read at a wavelength of 430 nm; and K was determined by flame photometry (Allen, *et al.*, 1974). The effect of treatments on yield was assessed by analysis of variance for a 2-factor factorial in a randomized complete block design.

RESULTS AND DISCUSSION

Fresh Weight Yields. Fresh weight yields of leaves and vines from 2-weekly harvests were significantly ($P = 0.01$) greater at 20 weeks after planting than yields from the 4-weekly harvests (Table 2). Since the period of significant fresh weight yield increase coincided with the time of greatest rainfall, it seems reasonable to assume that the crop achieved the greatest water use at this time. Compared to earlier periods of water shortage, increased temperatures, and drying winds typical of the dry season, there must have been increased transpiration, reduced evaporation, and increased water use efficiency at 20 weeks after planting. The highly significant fresh weight yields obtained from the 2-weekly har-

Table 2. The effect of mixed fertilizer levels (15-15-15 as $N\text{-}P_2O_5\text{-}K_2O$) and harvest intervals on the fresh weight yield (t/ha) of fluted pumpkin.

Harvest Interval (weeks)	Fertilizer Level (kg/ha)	Weeks After Planting					Total	Mean**
		8	12	16	20	24		
2*	0	0.59	1.37	2.48	0.76	3.22	8.42	1.68
	200	0.65	2.19	2.76	1.07	3.78	10.44	2.09a
	400	0.49	1.96	2.98	0.11	3.47	9.82	1.96a
4	0	0.33	1.49	2.26	0.59	1.98	6.64	1.33b
	200	0.42	2.06	5.17	0.62	3.09	11.36	2.27b
	400	0.52	1.80	3.76	0.54	2.85	9.47	1.89a

* For easy comparison with four weekly harvests, the yields for the two weekly harvests were recorded as totals of four weeks; thus, at 16 weeks after planting, 2.48 t/ha is the total for 14 and 16 weeks after planting.

** Means followed by the same letters do not differ significantly at $P = 0.05$, according to Duncan's Multiple Range Test.

vests point to the fact that total yield in some vegetables tends to decrease with an increase in the interval between harvests. These results are in accord with observations (Greensill, 1970) on *Basella alba* (Indian spinach) in which increased frequency of harvests led to increased yields. The results also confirm previous findings (Ossom, 1986) on the fluted pumpkin in which a reduced harvest interval caused profuse branching resulting in more vine and leaf growth from the 2-weekly harvests than from the 4-weekly harvests. The results of this work also agreed with observations (Thomas, 1965) that indicated that the more quickly vegetable plants grow, the larger their yield of leaves. The stimulatory effect of more frequent harvests appears to be associated with the frequent release from apical dominance (Meyer, *et al.*, 1960) in the vines, giving rise to more profuse branching, more production of leaves, and, consequently, increased fresh weight yields.

Fertilizer Effects. Fertilizer levels were not found to significantly affect total fresh weight yields, except at 20 weeks after planting (Table 2). The reason for this was not determined in this study. However, at about 15 weeks after planting, flowers of the fluted pumpkin start to form (Orgu, 1989). Translocation of nutrients out of the leaves into the flowers could have taken place at about 15 weeks after planting, and this movement could have adversely affected leaf and vine yield at 20 weeks after planting.

Earlier, workers at International Institute of Tropical Agriculture (1972) had shown that there were no significant effects of fertilizer levels on the total yield of jute, but greener and more attractive leaf blades were observed at higher fertilizer levels. At later harvests in this experiment, the older leaves on the plants in the unfertilized plots were chlorotic in pattern, indicating a lack of N in the tissues.

Table 3. The effect of mixed fertilizer levels (15-15-15 as $N\text{-}P_2O_5\text{-}K_2O$) and harvest intervals on N concentration (%) in the leaf blades of the fluted pumpkin. Each figure is the mean of three replicate determinations.

Harvest Interval (weeks)	Fertilizer Level (kg/ha)	Weeks After Planting						Mean	Std. Dev.
		8	10	12	16	20	24		
2	0	3.48	4.16	3.44	2.78	1.98	1.77	2.94	0.93
	200	4.47	4.47	5.04	4.86	3.45	3.81	4.40	0.63
	400	5.45	6.11	6.35	5.53	4.53	4.83	5.47	0.70
Mean		4.47	5.01	4.35	4.49	3.32	3.47		
Std. Dev.		0.99	1.00	1.46	1.43	1.28	1.56		
4	0	3.45	—	3.36	2.26	—	1.59	2.67	0.90
	200	4.47	—	4.91	4.58	—	3.09	4.26	0.80
	400	5.23	—	6.24	5.15	—	4.16	5.20	0.85
Mean		4.39	—	4.48	4.00	—	2.9		
Std. Dev.		0.89	—	1.44	1.53	—	1.29		

Table 4. The effect of mixed fertilizer levels (15-15-15 as $N\text{-}P_2O_5\text{-}K_2O$) and harvest intervals on P concentration (%) in the leaf blades of the fluted pumpkin. Each figure is a mean of three replicate determinations.

Harvest Interval (weeks)	Fertilizer Level (kg/ha)	Weeks After Planting						Mean	Std. Dev.
		8	10	12	20	22	24		
2	0	0.39	0.30	0.45	0.37	0.36	0.33	0.37	0.05
	200	0.36	0.30	0.43	0.39	0.34	0.31	0.36	0.05
	400	0.30	0.37	0.36	0.41	0.30	0.46	0.37	0.06
Mean		0.35	0.32	0.41	0.39	0.33	0.37		
Std. Dev.		0.05	0.04	0.05	0.02	0.03	0.08		
4	0	0.37	—	0.41	0.26	—	0.28	0.33	0.07
	200	0.35	—	0.36	0.32	—	0.30	0.33	0.03
	400	0.33	—	0.36	0.35	—	0.34	0.35	0.01
Mean		0.35	—	0.38	0.31	—	0.31		
Std. Dev.		0.02	—	0.03	0.05	—	0.03		

Table 5. The effect of mixed fertilizer levels (15-15-15 as $N\text{-}P_2O_5\text{-}K_2O$) and harvest intervals on K concentration (%) in the leaf blades of the fluted pumpkin. Each figure is a mean of three replicate determinations.

Harvest Interval (weeks)	Fertilizer Level (kg/ha)	Weeks After Planting						Mean	Std. Dev.
		8	10	12	20	22	24		
2	0	4.63	4.35	4.25	4.16	4.16	3.88	4.24	0.25
	200	4.56	4.97	4.69	4.44	4.16	5.25	4.67	0.39
	400	4.44	4.94	5.10	4.78	5.28	5.41	4.99	0.35
Mean		4.60	4.75	4.68	4.46	4.53	4.85		
Std. Dev.		0.10	0.35	0.43	0.31	0.65	0.84		
4	0	5.50	—	4.03	4.13	—	3.14	4.20	0.97
	200	4.25	—	4.41	4.28	—	4.08	4.23	0.14
	400	3.56	—	5.03	4.31	—	4.25	4.29	0.60
Mean		4.44	—	4.49	4.241	—	3.82		
Std. Dev.		0.98	—	0.50	0.10	—	0.60		

Foliar Concentrations of N, P, and K. Mineral concentrations in the leaf lamina (Tables 3-5) indicated that plants that received the higher levels of fertilizer also had higher N, P, and K concentrations as compared to plants that received lower amounts of fertilizer. As the fertilizer levels increased, the leaf blades became greener and more attractive. This change probably resulted from the increased mineral (particularly N) concentrations in the leaves of those plants that received higher amounts of fertilizer. Plants harvested every 2 weeks had a higher concentration of N, P, and K in their leaves than those cut every 4 weeks. Okugie and Ossom (1988), Omueti (1982a), Ossom, *et al.* (1983), and Schmid, *et al.* (1979) achieved similar results with other crop plants. In this work, the 2-weekly harvests continually gave more tender and fresher leaves in contrast to the 4-weekly harvests whose leaves were more fibrous. Omueti (1982b) reported that vegetable leaves cut at intervals of more than 2 weeks were higher in crude fiber than those cut at shorter intervals. From a dietary point of view, fluted pumpkin leaves should be harvested every 2 weeks, when they are most nutritious.

K concentration (Table 5), like N and P concentration, also decreased steadily with time, particularly from 12 weeks after planting. Similar observations had been made on other tropical vegetables (Omueti, 1977). The decreased mineral concentration could be associated with leaf aging and the movement of minerals from the leaves and vines to sites undergoing vegetative and reproductive growth (Orgu, 1989). K is rapidly translocated to meristems (Meyer, *et al.*, 1960). The decrease in K concentration in the leaves was probably due to such outward movement.

SUMMARY

This experiment was conducted to evaluate the influence of mixed fertilizer levels and harvest intervals on the fresh weight yield of the leaves and the N, P, and K concentrations in the leaves of fluted pumpkin planted in the dry season. The results of this research point to the need for farmers to fertilize fluted pumpkin with mixed fertilizer and to harvest the crop every two weeks in order to obtain high yield as well as tender and more nutritious leaves and vines.

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HYPER-Ia ANTIGEN EXPRESSION ON PERITONEAL MACROPHAGES CORRELATES WITH SEVERE *LEISHMANIA MAJOR* INFECTIONS IN MICE

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ABSTRACT: The role macrophages may play in the response of genetically susceptible and resistant strains of mice toward *Leishmania major* infections was studied. When infected subcutaneously, the highly susceptible Balb/c mice developed high levels of Ia^+ peritoneal macrophages which paralleled the development of severe, systemic disease. Whereas normal Balb/c mice had between 5-10% Ia^+ peritoneal macrophages, animals with severe leishmanial infections had 30-40%. The increased level of systemic macrophage activation in infected animals, which was detected as early as three weeks post infection, was not accompanied by an increase in total macrophage numbers in the peritoneal cavity. In contrast, the resistant C57B1/6 strain did not show increased levels of Ia^+ bearing macrophages following infection, even though mild, systemic infections did occur in these animals. Balb/c mice protected against serious, progressive infections by prophylactic treatment with cyclosporin A did not develop increased levels of Ia^+ peritoneal macrophages. *In vitro*, these phagocytes exhibited decreased phagocytic activity toward both *L. major* and *Candida albicans*, although their ability to destroy *L. major* did not seem to be impaired.

KEYWORDS: *Candida albicans,* cyclosporine, hyperactivation, Ia, *Leishmania major, Listeria monocytogenes,* macrophages, and mice.

INTRODUCTION

Depending on their genetic background, inbred mice vary markedly in their susceptibility to disease caused by *Leishmania major*. The Balb/c mouse strain is the most susceptible, with many other strains, including the C57B1/6 mice, showing considerable resistance (Mitchell, *et al.,* 1987). In general, the ability to mount an effective cell-mediated immune response appears to be responsible for recovery from infection, whereas antibodies seem to play little or no role in controlling the disease (Liew, *et al.,* 1984; Sadick, *et al.,* 1987). Although the reasons for the exquisite susceptibility of Balb/c mice toward this parasite are not clear, they do not include a failure to recognize or respond to infection. On the contrary, susceptible mice produce high antibody titers (Olobo, *et al.,* 1980; Sadick, *et al.,* 1987) and a rapid, hyper-expansion of activated $L3T4^+$ lymphocytes (Milon, *et al.,* 1986), which can transfer delayed-type hypersensitivi-

ty without establishing effective immunity (Dhaliwal, *et al.,* 1985). These cells have been shown to exacerbate disease when transferred to *L. major*-infected syngeneic mice (Titus, *et al.,* 1984). Several researchers (Milon, *et al.,* 1986; Modabber, *et al.,* 1987) have suggested that Balb/c mice are hyper-reactive rather than deficient in their responses to leishmanial infection. Their view is supported by the fact that various immunomodulatory or even immunosuppressive procedures, which affect a variety of cell types, render these mice more resistant to serious disease following infection. These procedures include prophylactic treatment with sublethal irradiation, anti-IgM antibody, anti-L3T4 antibodies, or, in our own laboratory, cyclosporin A (Howard, *et al.,* 1981; Sacks, *et al.,* 1984b; Titus, *et al.,* 1985; Behforouz, *et al.,* 1986). If given for only one week at the time of infection, cyclosporin A protects Balb/c mice from severe infections and renders them immune to reinfection (Behforouz, *et al.,* 1986).

Not only is there evidence of hyperactivity in the early stages of the infection in Balb/c mice, but there is also considerable symptomology and immunopathology related to an inappropriate immune response as the disease becomes progressively more severe. Lymphadenopathy, splenomegaly, hypergammaglobulinemia, and autoimmune antibodies characterize the late stages of the disease both in susceptible mice and in humans suffering from visceral leishmaniasis (Veres, *et al.,* 1977; Rezai, *et al.,* 1978; Djoko-Tamnou, *et al.,* 1981; Kharazmi, *et al.,* 1982; Behforouz, *et al.,* 1983).

The underlying reason for this excessive, inappropriate response to leishmanial infection is not clear but may be related to a faulty macrophage-T cell interaction. In recent years, the important immunoregulatory role of macrophages and other accessory cells has become increasingly clear (Unanue and Allen, 1987). A sensitive measure of the level of accessory cell activation and the ability to stimulate antigen-specific lymphocytes is the expression of the Class II MHC antigens, Ia, on the cell surface. Indeed, enhanced expression of Ia antigen on accessory cells has been associated not only with an active immune response to an acute infection in mice (Beller, *et al.,* 1980) but also to the immunopathology observed in several models of murine autoimmunity (Lu and Unanue, 1982; Monroe, *et al.,* 1985; Rosenberg and Kotzine, 1989) and to the dysregulation or dysfunction observed in AIDS (Buhl, *et al.,* 1993).

In order to determine the possible role of macrophage activation in the hyperactivity of Balb/c mice toward *L. major*, the level of Ia expression on peritoneal macrophages was determined in infected mice of both the Balb/c and the resistant C57B1/6 strains over time. Although C57B1/6 mice do develop mild systemic infections, including lymph node and splenic involvement, they maintain normal levels of Ia^+ peritoneal macrophages throughout the infection. Balb/c mice, on the other hand, develop an abnormally high level of Ia^+ peritoneal macrophages early after infection, and the number continues to increase slowly throughout the infectious process. However, Balb/c mice protected from serious disease by prophylactic treatment with cyclosporin A continuously maintain normal levels of Ia^+ peritoneal macrophages. Interestingly, the Ia^+ macrophages

retrieved from untreated, infected Balb/c animals with a heavy parasite burden did not harbor any *Leishmania* parasites but appeared to be functionally impaired with a generalized defect in phagocytic capacity.

MATERIALS AND METHODS

Animals. The Balb/c and C57B1/6 mice used in this study were raised in our own breeding facilities from stock originally purchased from Harlan-Sprague Dawley, Inc. (Indianapolis, Indiana). Experiments were performed with animals of either sex, 8 to12 weeks in age.

Culture of *Leishmania major* and Infection of Mice. *Leishmania major* (Freidlin strain, NIH) was kindly provided by Dr. D. Sacks of NIH and was grown in medium 199 with 20% fetal bovine serum at 24° to 26° C. After 5 to 6 days, these promastigotes reached stationary phase and, as demonstrated by Sacks and Perkins (1984a), were highly infective for Balb/c mice. All mice were infected in the left hind foot pad with 1 x 10^6 stationary phase promastigotes of *L. major*. The size of the swelling or lesions which developed was estimated by measuring the diameter of the center of the foot (top to bottom) using vernier calipers. By 8 to 12 weeks after infection, most of the untreated Balb/c animals had lost their infected foot due to destructive necrosis.

Cyclosporin A Treatment. Cyclosporin A (CsA) was generously provided by Sandoz Ltd. (East Hanover, New Jersey) in the oral solution, Sandimmune®. For oral treatment, which was found to cause less toxicity in treated mice, the animals were given the undiluted oral solution (100 mg/ml) at 150 mg/kg twice daily for seven consecutive days beginning one day before infection with *L. major*. Depending on the weight of the mouse, between 0.3-0.5 ml of the Sandimmune solution was delivered orally using a 200 µl pipettor with a plastic tip. Infected control animals were given olive oil in the same manner.

Peritoneal Macrophage Collection. Peritoneal exudate cells (PEC) were collected aseptically by lavage from normal or infected mice using RPMI 1640 medium with 5% fetal bovine serum (FBS) and antibiotics. The cells were washed once, and their concentration in the above medium was adjusted to approximately 1-3 x 10^6 cells/ml. The cells were then cultured for 2 to 3 hr in 1 ml volumes in 24-well microtiter plates (Falcon 3047) containing a 9 x 9 glass coverslip (Bellco Biotechnology, Vineland, New Jersey). The microtiter plates were centrifuged for 5 minutes at 500 g to aid the adherence of the cells to the coverslips. Following a 2-hour incubation at 37° C in 5% CO_2, the coverslips with the PEC were removed by forceps and gently but exhaustively washed with saline from a squeeze bottle to remove any non-adherent cells. Cells collected in this way were found to be > 98% macrophages by staining for the presence of alpha-acetate-esterase (Manca, *et al.*, 1985), using a staining kit obtained from Sigma Chemical Company (St. Louis, Missouri).

Detection of Ia Antigens. Ia antigens on peritoneal macrophages of either Balb/c or C57B1/6 mice were detected by an indirect immunofluorescence assay using either the monoclonal antibody MK.D6 specific for Ia^d or the mon-

oclonal antibody 34-5-3 specific for Ia^b and an affinity purified fluorescein conjugated $F(ab')_2$ rabbit anti-mouse Ig (Pel-freeze Biologicals, Rogers, Arkansas). Both monoclonal antibodies were used as 1:10 dilutions of culture supernatants (diluent: medium plus 10% rabbit serum plus 10 mg/ml bovine serum albumin) kindly provided by Dr. E. Unanue (Washington University, St. Louis, Missouri). The conjugate was used at a final concentration of 85 µg/ml. The staining procedure used was essentially that of Beller, *et al.* (1980) with slight modification. Briefly, the washed coverslips coated with the adherent peritoneal cells were placed in clean microtiter wells with approximately 1 ml of freshly prepared 1% paraformaldehyde for 15 minutes at room temperature. Then, the coverslips were washed with saline and placed cell side down within the depression of a hanging drop slide containing 20 µl of either anti-Ia^b, anti-Ia^d, or diluent alone. These slides were placed on ice for 30 minutes, washed, and placed cell side down in the depression of a clean hanging drop slide containing 20 µl of the fluorescein conjugate on ice for another 30 minutes. The coverslips were washed again and placed singlely with the cell side up in the wells of microtiter plates containing 1 ml of phosphate buffered saline until the time of examination. The macrophages were examined at 400x with both bright light illumination and epifluorescent illumination using a Zeiss microscope after placing the coverslips cell side down in PBS in the depression of a hanging drop slide. In all experiments, duplicate coverslips were prepared for each experimental animal, and a total of at least 800 macrophages was counted on both coverslips as well as the number of brightly stained cells with distinct perimeters which were considered Ia positive. The specificity of the reaction of the anti-Ia and the fluorescein labeled $F(ab')_2$ anti-Ia was determined in the following manner. First, some of the resident peritoneal macrophages from normal C57B1/6 ($H\text{-}2^b$) were stained when anti-Ia^b antibodies were used but were not stained when anti-Ia^d antibodies were applied. Likewise, positive staining of macrophages from Balb/c animals ($H\text{-}2^d$) occurred only when anti-Ia^d but not anti-Ia^b antibodies were used. Second, the $F(ab')_2$ conjugate by itself did not stain the cells when diluent was used in place of anti-Ia antibody. Finally, Ia-positive macrophages represented only a small fraction of the adherent cells from normal animals, suggesting that the uptake of conjugate was a cell-specific reaction.

Spleen, PEC, and Lymph Node Involvement. The popliteal lymph nodes from the left leg and the spleens of infected mice were removed aseptically following collection of the PEC and were weighed. The spleens were placed in a pre-weighed sterile petri dish with HBSS, weighed, and then ground between two frosted-end glass slides. The resulting cell suspension was pelleted, resuspended in 10 ml of medium 199 plus 20% FBS for culture of *Leishmania*, and allowed to incubate at 25° C in a 25 cm^2 culture flask. Occasionally, suspensions of PEC collected from infected mice were also cultured and incubated in the same manner in 5 ml of the leishmanial culture medium. All cultures were checked daily for the presence of *L. major* promastigotes by a thorough microscopic

examination of a 20 µl ml sample. Negative cultures were discarded after 14 days.

Anti-Microbial Activity of Macrophages. PEC were collected aseptically (see above), washed, and their concentration was adjusted to 3 x 10^6/ml in medium plus 10% FBS. The cells were added in 400 µl volumes to the wells of eight-well Lab-Tek® culture slides. The cells were allowed to adhere overnight at 37° C in %5 CO_2 and then washed several times to remove non-adherent cells. Duplicate cultures of adherent macrophages were then infected with 300 µl of either 1 x 10^7/ml stationary phase *L. major* promastigotes in medium 199 with 20% FBS at 37° C in 5% CO_2 for two hours or 5 x 10^6/ml *Candida albicans* in RPMI medium plus 10% FBS for one hour. Following incubation, any non-ingested microbes were removed by extensive washing of the culture wells, and the cells were reincubated. After either two hours or several days in culture, the plastic wells were removed, and the slides were fixed in methanol, Giemsa stained, and examined microscopically for intracellular yeast or amastigotes. Both the percentage of infected macrophages and the number of parasites per macrophage were determined for each experimental group. A minimum of 400 macrophages were examined per culture, and the calculations were made as follows:

$$\frac{\text{number of macrophages bearing microbes}}{\text{number of total macrophages counted}} \times 100 = \text{Percent infected macrophages}$$

$$\frac{\text{number of intracellular microbes observed}}{\text{number of total infected macrophages}} \times 100 = \text{Mean number of microbes per infected microphage}$$

RESULTS

Hyper-Ia^d Expression in Infected Balb/c Mice. In preliminary experiments, peritoneal macrophages obtained from four Balb/c mice infected sixteen weeks previously with *Leishmania major* were found to express abnormally high levels of Ia^d in comparison to age-matched controls (i.e., 47 ± 11% vs 12 ± 4%). Although older mice generally have somewhat higher levels of Ia$^+$ peritoneal macrophages than younger mice (Beller, *et al.,* 1980), in repeated trials nearly half of the adherent cells obtained from the diseased animals consistently expressed Ia$^+$. The spleen weights of the diseased animals were nearly eight times heavier than normal with three times the monocytic cell number. Although the percentage of Ia-bearing macrophages detected in the spleens of the infected animals was high (> 50%), this value falls within the reported normal range (Cowing, *et al.,* 1978), and the percentage of Ia$^+$ adherent splenic cells from normal animals did not differ perceptibly from their percentage in the diseased animals.

In order to determine whether the activated state of the peritoneal macrophages was a late-developing feature of severe disease, Balb/c mice were infected

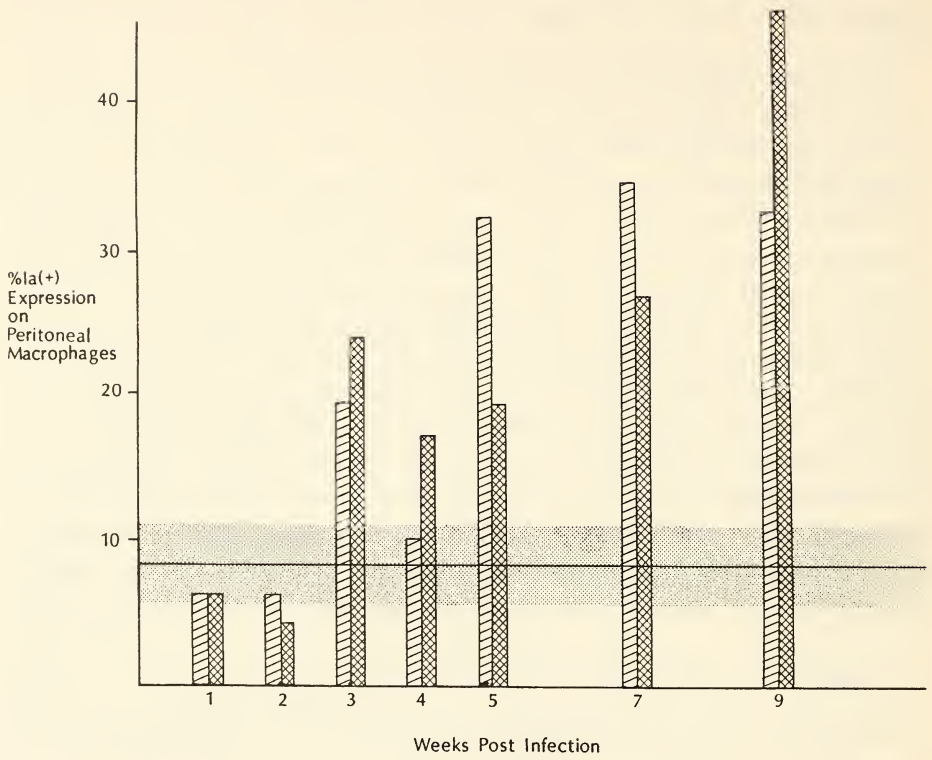

Figure 1. Balb/c mice infected with *Leishmania major* have increasing levels of Ia positive peritoneal macrophages. At various time intervals following infection with 1 x 10^6 promastigotes, two mice were sacrificed, and the percentage of Ia-bearing macrophages was determined for each (▨,▩). The mean ± standard deviation of eight normal, aged-matched controls is shown as the horizontal line within the shaded area.

with *L. major,* and the percentage of Ia^+ macrophages was determined at various time intervals following infection. Although the number of macrophages expressing Ia remained within the normal range of age matched controls for two weeks following infection, at three weeks post infection the individual mice began to show elevated levels of Ia expression (Figure 1). Whereas the level of Ia^+ cells was greater than 30% in the infected animals by week 9, the levels in normal, age-matched controls remained between 5% and 11%. At no time could *L. major* be recovered from the peritoneal macrophages of infected Balb/c animals under conditions permissive to outgrowth of *Leishmania* amastigotes, even in severely ill animals having a heavy parasite burden in the spleen (data not shown).

Comparison of Macrophage Activation in Resistant and Susceptible Mice During Infection. Although C57Bl/6 mice developed infections with *L. major* as evidenced by the development of some foot pad swelling, significant lymphadenopathy, mild splenomegaly, and rapid metastasis of *L. major* to the

Table 1. Correlation of the expression of Ia on peritoneal macrophages with various disease parameters over time in Balb/c and C57Bl/6 mice infected with *L. major*[1].

Mouse Strains	Days Post Infection	Number of Animals	% Ia$^+$ Peritoneal Macrophages[2]	Foot Pad Size (cm)[2]	Lymph Node Weight (mg)[2]	Spleen Weight (g)[2]	*L. major* Positive Spleen Culture
Balb/c	0	6	8.2 ± 2.7	0.23 ± 0.01	1	0.12 ± 0.02	-
C57B1/6		4	6.9 ± 1.0	0.23 ± 0.02	1	0.07 ± 0.01	
Balb/c	7 - 14	7	6.8 ± 1.8	0.30 ± 0.05	7 ± 6	0.11 ± 0.02	4/7
C57B1/6		3	8.1 ± 0.7	0.35 ± 0.07	1	0.14 ± 0.07	2/3
Balb/c	21 - 30	12	13.1 ± 4.9*	0.43 ± 0.1	20 ± 10	0.11 ± 0.02	12/12
C57B1/6		8	7.2 ± 1.9	0.35 ± 0.07	28 ± 18	0.13 ± 0.09	8/8
Balb/c	35 - 42	6	20.2 ± 7.2*	0.67 ± 02	71 ± 26	0.28 ± 0.12	6/6
C57B1/6		4	6.4 ± 1.5	0.30 ± 0.01	37 ± 4	0.10 ± 0.03	4/4
Balb/c	49 - 60	6	27.2 ± 5.9**	NF[3]	98 ± 17	0.44 ± 015	6/6
C57B1/6		4	9.5 ± 0.7	0.28 ± 0	45 ± 18	0.05 ± 0.01	4/4
Balb/c	63 - 84	7	31.8 ± 12.7*	NF[3]	140 ± 48	0.55 ± 0.23	7/7
C57B1/6		6	7.5 ± 3.35	0.26 ± 0.02	55 ± 5	0.06 ± 0.02	5/6

[1] These results represent three experimental trials. The mice were infected and followed as described in the *Materials and Methods*.
[2] Mean ± Standard Deviation.
[3] No foot due to necrotic destruction.
* $p < 0.01$; Unpaired Student's t testing was used for analyzing the difference between the mean percentages of Ia positive cells in the two groups of mice.
** $p < 0.001$.

spleen, the percentage of peritoneal macrophages which expressed Ia^b never rose over normal levels throughout the infection period (Table 1). Interestingly, as late as 2 to 3 months post infection, when foot pad size and spleen weight had essentially returned to normal, 5/6 of the C57Bl/6 animals examined still harbored residual, viable *Leishmania* in the spleen, and the draining popliteal lymph nodes were still enlarged. Thus, resistance to and successful recovery from this parasite occurs in spite of a chronic, metastatic infection.

In Balb/c mice, the development of lymphadenopathy, splenomegaly, and foot pad swelling was nearly parallel to that in the C57Bl/6 mice for one month post infection. In fact, early in infection, average spleen and lymph node weights were somewhat larger in the C57Bl/6 mice than in the Balb/c mice. In contrast, the increase in Ia expression by peritoneal macrophages was again observed to appear as early as three weeks post infection in the susceptible mice, considerably before the appearance of splenomegaly, severe foot pad swelling, or ulceration. The average level of Ia$^+$ macrophages also appeared to increase as the infection progressed in the Balb/c mice. However, no consistent rise or fall in the total numbers of cells in the peritoneal cavities of either group of mice was noted during infection (data not shown).

Ia Expression and Disease Progression in Cyclosporin A Protected Balb/c Mice. In order to see whether or not hyper-Ia expression occurs during *L. major*

infections in susceptible Balb/c animals protected from serious disease, two groups of Balb/c animals were infected with *L. major*, and one group was prophylactically treated with CsA either subcutaneously or orally for seven days. Infected mice treated with CsA developed minimal foot pad swelling, minor spleen enlargement, and reduced lymphadenopathy when compared to the control mice (Figure 2). In addition, the percentage of Ia^+ peritoneal macrophages in these protected animals did not rise above normal levels throughout the ten-week post infection test period. Indeed, the pattern of disease symptoms and level of Ia on peritoneal macrophages observed in these CsA-treated animals was very similar to that observed in infected C57Bl/6 animals. In these studies, non-protected Balb/c animals once more showed a very early increase in the percentage of Ia^+ macrophages in response to *L. major* infection. As with the other infected groups, *L. major* could be cultured from the spleens of the drug-treated mice as early as one week and as late as three months post infection (data not shown).

As the above studies were continued for only ten weeks, several animals treated with the drug were maintained and compared to non-treated animals several months post infection. Although animals infected for three to four months without CsA treatment were severely diseased and had an average level of Ia-bearing macrophages of > 35%, the animals prophylactically protected with cyclosporin appeared essentially normal, and their level of Ia^+ peritoneal macrophages remained normal (data not shown.).

Phagocytic and Microbicidal Ability of Balb/c Mice Infected with *L. major*. Beginning as early as one month post infection, cultured macrophages obtained from the peritoneal cavity of *L. major*-infected mice were found to be consistently less active phagocytically toward *L. major* than normal PEC (Table 2). Compared to macrophages obtained from normal age-matched Balb/c animals, the percentage of cultured macrophages from infected animals bearing amastigotes following a 2-hour incubation with *L. major* was lower than in normal PEC cultures. This impairment was also observed in phagocytosis of the non-specific antigen, *Candida albicans* (Figure 3). The numbers of microbes (both *L. major* and *C. albicans*) phagocytosed per infected cell (rather than total cells) was also considerably lower throughout the infection period , indicating that all cells, even those capable of phagocytosis, had a generalized lower capacity for phagocytosis. Although the phagocytic potential of the macrophages from infected animals was less than normal, the leishmanicidal capacity *in vitro* appeared to be unaltered. In repeated trials, peritoneal macrophages from infected animals were found to be able to reduce their parasite burden at rates comparable to those of the normal macrophages. Figure 4 represents the results of one of these trials and demonstrates that, although the mean number of *L. major* taken up per macrophage was > 3 for the normal animals after 3 hours, the macrophages from infected animals had taken up < 1.5 parasites per cell. After four days incubation, however, cells from both the normal and diseased animals had reduced their parasite burden by at least 87%. Of course, the original para-

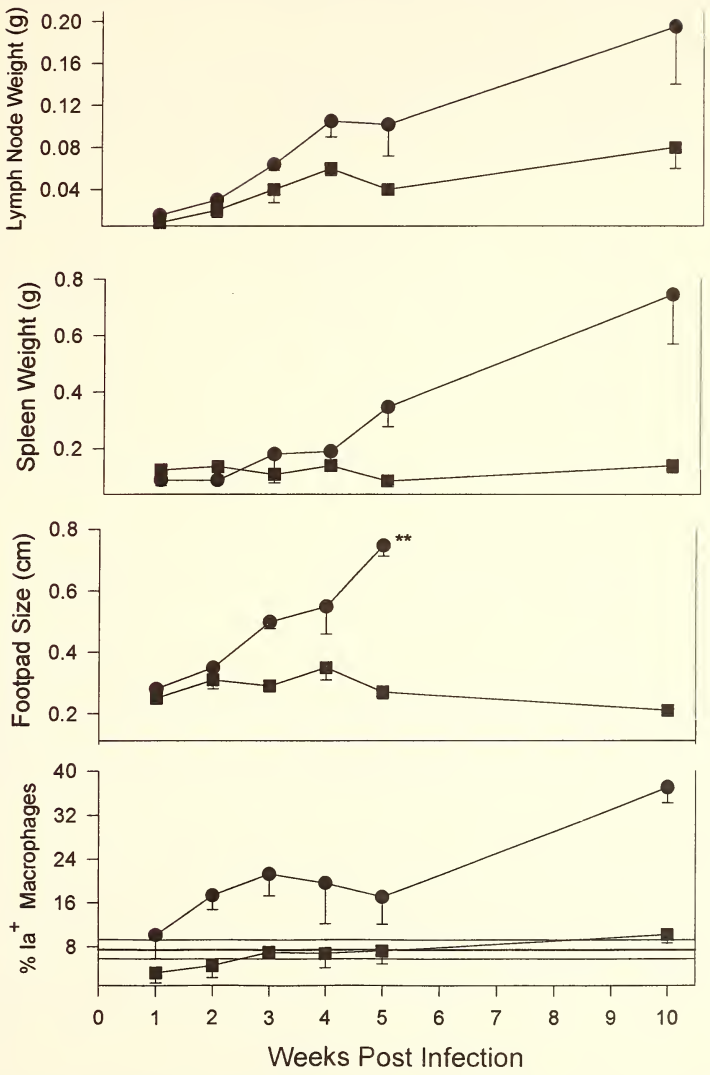

Figure 2. Infected Balb/c mice protected against severe disease by prophylactic treatment with CsA do not develop increased levels of Ia-bearing peritoneal macrophages. The figure reflects the combined results of three separate trials. In each trial, two groups of at least 12 mice each were infected with 1 x 10^6 *Leishmania major* in the left hind foot pad. One group received CsA for seven days as described in the *Materials and Methods* (■); the other infected group was not treated (•). At different intervals for a period of ten weeks, two to four mice in each group were sacrificed, and determinations of spleen and lymph node weight, foot pad size, and the percentage of Ia-bearing macrophages were made. Each point on the figure represents the mean ± standard deviation of the determinations for each time period. No foot pad measurements could be taken past this time point (**) because of necrotic destruction of the foot. The mean percent Ia^+ macrophages from 8 uninfected animals ± standard deviation is shown as the horizontal line with two surrounding lines. The normal values for Balb/c foot pad size and spleen weight are 0.25 ± 0.01 and 0.1 ± 0.01, respectively.

Table 2. Phagocytic capacity of peritoneal macrophages from infected Balb/c mice toward *L. major*[1].

Months Post Infection[2]	Source of Macrophages	% Macrophages Bearing *L. major*[3]	*L. major* /Infected Macrophage[4]
Experiment 1			
1	Normal	44 ± 7	2.1 ± 0.3
	Infected	18 ± 2	1.5 ± 0.3
2	Normal	50 ± 1	2.7 ± 0.7
	Infected	29 ± 8	2.4 ± 0.1
3	Normal	73 ± 2	3.7 ± 0.6
	Infected	51 ± 2	2.6 ± 0.6
4	Normal	43 ± 5 3	1 ± 0.2
	Infected	23 ± 4 1	8 ± 0.4
Experiment 2			
1	Normal	67 ± 6	2.6 ± 0.2
	Infected	45 ± 7	2.0 ± 0.1
3	Normal	59 ± 1	4.0 ± 0.9
	Infected	21 ± 13	2.3 ± 0.6

[1] PEC from each of 3 animals per group were individually adjusted to 1-2 x 10^6 cells/ml and allowed to adhere overnight in duplicate in Lab-Tek culture slides. The washed cells were infected with 1 x 10^7/ml *Leishmania major* for a period of 2 hours at 37° C in 5% CO_2 and were washed thoroughly to remove non-phagocytosed microbes. The slides were immediately air dried and stained with Geimsa before microscopic examination.

[2] Balb/c animals were infected with *L. major* as described in the *Materials and Methods*. The normal animals were age-matched Balb/c mice.

[3] The percent of stained macrophages bearing intracellular *L. major* was determined as described in the *Materials and Methods*. The results are shown as the mean percent infection of cells from 3 animals per time point. The PECs from infected animals displayed at least a 2-fold higher level of Ia^+ cells at all time points over those from normal animals.

[4] The number of *L. major* per infected macrophages was determined as described in the *Materials and Methods*. The results are shown as the mean number of amastigotes per infected cell ± SD per time point.

site burden/cell for the cells of the infected host was smaller, and the cultures were incubated for several days outside the potentially inhibitory surroundings of the diseased animal.

DISCUSSION

The data reported here demonstrate that Balb/c mice infected with *Leishmania major*, which are destined to develop severe, overwhelming infections, also develop abnormally high levels of Ia positive peritoneal macrophages early in the infection. This apparent systemic activation of macrophages distant from the original lesion continues for the remainder of the infection and tends to increase over time. In contrast, genetically resistant mice do not develop increased levels of Ia-bearing macrophages at any time in response to the parasite even though they develop mild systemic infections. Interestingly, the percentage of

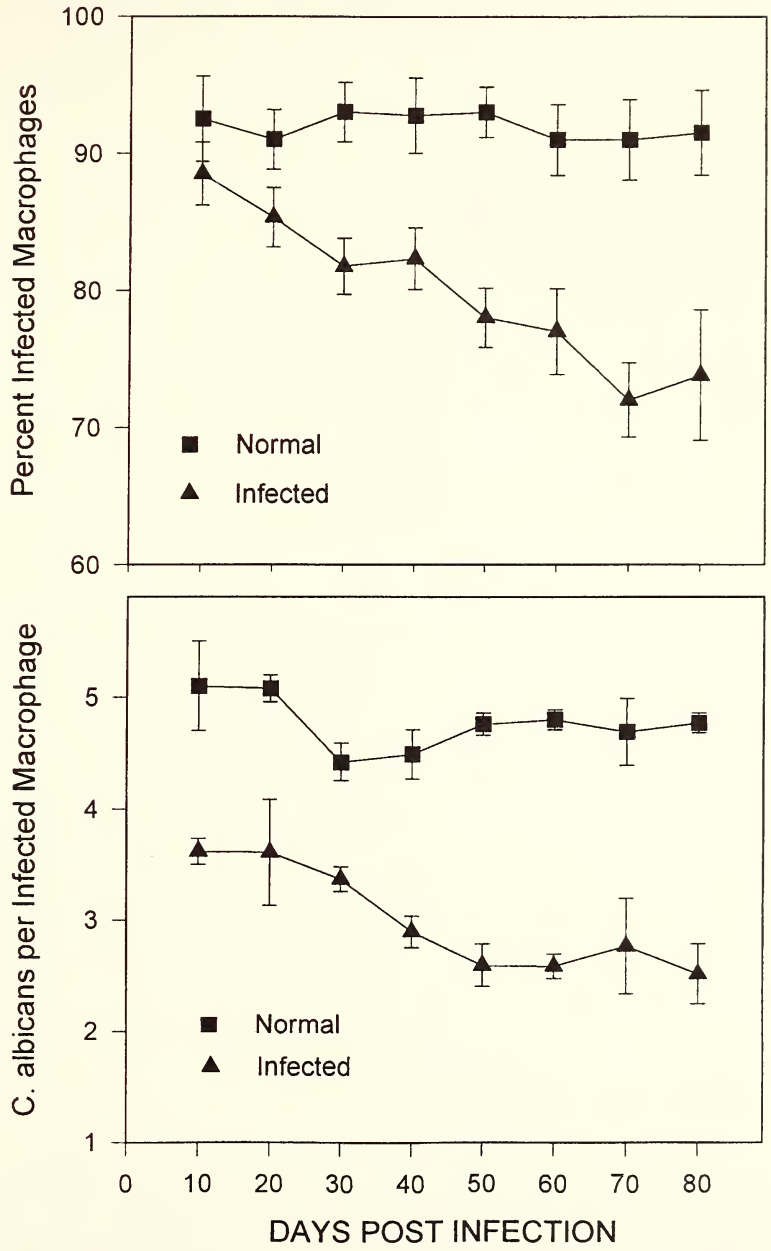

Figure 3. Peritoneal macrophages from *L. major*-infected animals exhibit a general defect in phagocytosis. Adherent PEC from each of three *L. major*-infected or normal age-matched Balb/c animals were cultured, infected, and stained individually in duplicate as described in Table 2 except that the washed cells were exposed to 5 x 10^6/ml *Candida albicans* rather than *L. major* for a period of 2 hours. The percentage of stained macrophages bearing intracellular *C. albicans* was determined as described in the *Materials and Methods*. The results are shown either as the mean percent infection of cells from three animals (A) or the mean number of *C. albicans* per infected macrophage (B) per time point ± standard deviation.

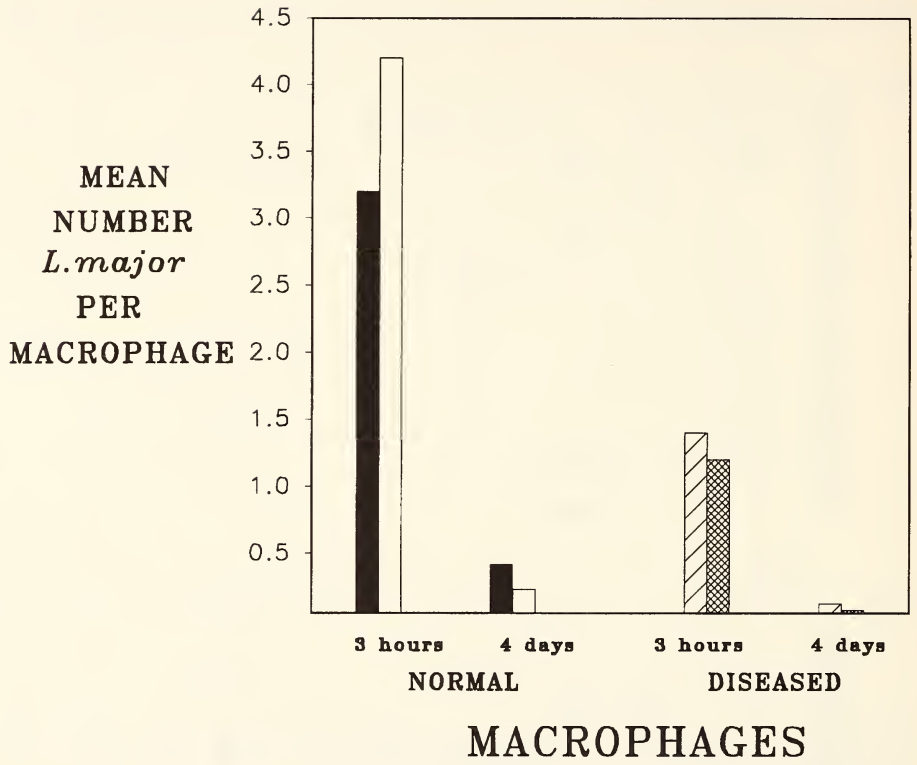

Figure 4. Peritoneal macrophages from *L. major*-infected animals do not appear to have impaired leishmanicidal capacity upon *in vitro* cultivation. Adherent PEC from each of two animals infected three months previously (▨,▩) and two normal animals (■,□) were cultured individually in quadruplicate as described in Table 2 and infected and incubated with 1 x 10^7/ml *L. major* for a period of three hours. After a thorough washing, duplicate slides for each animal were immediately stained and examined microscopically, while two others were reincubated for a period of four days at 37° C in 5% CO_2 before staining and examination. The mean number of *L. major* amastigotes per macrophage was determined as described in the *Materials and Methods*.

MHC class II bearing cells did not perceptibly increase in the spleens of the infected Balb/c animals, even though considerable splenic and lymph node enlargement did occur during the infection. The rise in Ia expression in infected Balb/c animals does not appear to be an irrelevant nor trivial difference between the two strains of mice, since Balb/c mice protected from serious disease by cyclosporin treatment also fail to develop increased levels of Ia-bearing macrophages at any time following infection. Thus, there appears to be a direct correlation between progressive disease and systemic hyper-Ia expression.

The systemic increase in Ia expression in mice has been observed in a number of disease states, including *Listeria monocytogenes* infection (Beller, *et al.*, 1980), autoimmune disease (Lu and Unanue, 1982; Rosenberg and Kotzin,

1989), and tumor-bearing animals (Evans, *et al.,* 1986). In all cases, the increased level of Ia-bearing macrophages was associated with an ongoing, active, immune response, and, in the case of infection and autoimmune models, the hyper-Ia expression was associated with severe disease. Recently, Buhl, *et al.* (1993) reported that class II MHC molecules are expressed more frequently and heavily on alveolar macrophages from asymptomatic HIV-infected individuals; they suggested that this upregulation was further evidence of the immune derangement, dysfunction, and deficiency observed in the pre-AIDS condition and in AIDS itself (Edelman and Zolla-Pazner, 1989). The development of abnormally high levels of Ia expression on peritoneal macrophages in mice with severe leishmanial infections may also indicate a role for these activated macrophages in the pathogenesis of murine leishmaniasis. Although the reason(s) for the failure of certain strains of mice to inhibit leishmanial infections is (are) still unclear, the failure may be related to an inappropriate stimulation of certain helper T lymphocyte subpopulations, which may lead to an exacerbated, rather than controlled infection (Titus, *et al.,* 1984; Louis, *et al.,* 1987). The preferential induction of certain subpopulations of T cells may be related either causally or secondarily to the presence of systemic, hyperactivated macrophages.

The results obtained in this study show that the level of macrophage activation in the peritoneum of an infected susceptible animal is abnormally high and becomes so relatively early in the infection before severe symptoms are evident. Whether or not this abnormality is central to the immune defect in these animals or is a consequence of stimulation by an activated T cell population is unclear. In murine leishmaniasis, the Th2 subpopulation of $L3T4^+$ cells appears to be preferentially stimulated in susceptible animals, whereas the Th1 helper subset is found to expand in resistant animals (Heinzel, *et al.,* 1989). The Th2 subset appears to uniquely secrete IL-4, IL-5, whereas the Th1 subset secretes IL-2 and γ-IFN (Mosmann, *et al.,* 1986). As γ-IFN is thought to be the central lymphokine responsible for activating macrophages to kill *Leishmania* amastigotes, the presence of a Th2 T cell response leading to IL-4 rather than γ-IFN production would be counterproductive for the murine host. Indeed, investigators have shown that there is a reciprocal expression of interferon-γ or IL-4 during resolution or progression of murine leishmaniasis (Heinzel, *et al.,* 1989). Perhaps, the hyper-Ia antigen expression noted in this study of infected Balb/c animals is induced and maintained by the expanded Th2 clone which produces an inappropriate balance of critical lymphokines, including an excessive amount of IL-4. This lymphokine has been shown to be a potent inducer of MHC Class II expression of lymphoid cells, including macrophages (Stuart, *et al.,* 1988; Crawford, *et al.,* 1987; and TeVelde, *et al.,* 1988).

Several investigators (Preston, *et al.,* 1978; Colle, *et al.,* 1983; Modabber, 1987) have suggested that an underlying reason for the susceptibility of Balb/c animals is hyper-reactivity toward the parasite, which leads to a generalized inflammatory response characterized initially by an inappropriate immune reactivity to *Leishmania* as well as other antigens. The fact that many types of pro-

phylactic immunosuppressive treatments, which decrease the activity or numbers of B cells, T cells, and even macrophages, induce some level of resistance in susceptible animals offers support for this view (Howard, *et al.,* 1981; Sacks, *et al.,* 1984b; Titus, *et al.,* 1985; Behforouz, *et al.,* 1986). Indeed, in many respects, the late stages of leishmanial disease in susceptible animals parallels that seen in MRL/1pr autoimmune mice. MRL/1pr mice develop spontaneous autoimmune disease with the production of a constellation of autoantibodies, hypergammaglobulinemia, increased helper cell activity, and massive spleen and lymph node enlargement. These mice also display an increased, systemic expression of Ia^+ on their peritoneal macrophages (Lu and Unanue, 1982). Hypergammaglobulinemia, splenomegaly, lymphadenopathy, and autoantibodies characterize systemic leishmaniasis in mouse and man (Djoko-Tamnou, *et al.,* 1981; Kharazmi, *et al.,* 1982). Lu and Unanue (1982) have suggested that lymphokine secreting T cells in MRL/1pr mice activate a large number of macrophages to express Ia which, in turn, may enhance T cell activities thus establishing a cycle of macrophage-T cell interactions that aggravate the hyperactive autoimmune responses and lymphoproliferation. A very similar situation may also occur in systemic leishmaniasis with an initial hyper-reactivity to antigen expanding into a destructive autoimmune response. The fact that the levels of Ia^+ macrophages in the peritoneum become elevated during infection only in susceptible animals may help us understand the etiology of the autoimmune component of leishmanial disease. Our finding that this population of heightened Ia-bearing cells was also severely compromised in their phagocytic ability toward both *L. major* and *C. albicans* may also be related to the profound failure to control the systemic spread and proliferation of the parasite in susceptible animals. Although these cells, shortly after removal from the host, were less capable phagocytically, their microbicidal capability after several days in culture appeared normal. Perhaps these cells regain normal cidal function following removal from the environment of the infected host and several days of *in vitro* culture. *In vivo*, the macrophage dysfunction may also extend to leishmaniacidal activity, particularly as the internal milieu of the host may include inhibitory lymphokines such as IL-4, which have been shown to impair phagocytic activity (Lehn, *et al.,* 1989). Panosian and Wyler (1983) reported that peritoneal macrophages from the genetically resistant C57Bl/6 mice infected with *L. major* are phagocytically less active toward *L. major* but not latex beads or opsonized SRBC during the first month of infection. This defect resolved as the animals recovered from their infections. The abnormally low phagocytic activity observed in the present study in susceptible Balb/c animals appears to be significantly different; i.e., there is a generalized reduction in phagocytosis, and there is no recovery. This defect in peritoneal macrophage activity concurrent with excessive Ia expression may reflect the systemic, non-protective hyperactivation observed in these animals.

The ability of cyclosporin A to prophylactically protect susceptible animals from severe infection is somewhat surprising in that CsA has been shown to inhibit production of both IL-2 and γ-IFN; it would seem that this drug would

exacerbate rather than promote healing of the infection. In order to protect animals, however, cyclosporin A is given only briefly at the beginning of the infection. If given later, following appearance of the lesion, CsA does indeed exacerbate the disease (Behforouz, *et al.,* 1986). The ability of a brief, intense treatment with cyclosporin A to promote a protective immune response only at a very early stage in infection would seem to indicate that the susceptibility of Balb/c mice to *L. major* results primarily from a flawed induction phase of the immune response. Thus, prophylactic CsA treatment may suppress irreversibly the hyperactive or unbalanced immune response initially induced by first exposure to leishmanial antigens. This effect might be accomplished by the selective suppression of the Th2 helper subset which appears to inappropriately expand in these animals or by an overall suppression of all T helper activity early in the infection. One of the critical consequences of this T cell suppression might be the suppression or modulation of MHC class II antigens, namely Ia, on the surface of the antigen-presenting cells. Indeed, CsA has been shown to block the induction of MHC class I and II antigens in experimental GVHD (Autenreid and Halloran, 1985) and to inhibit increased expression of MHC products in MRL/1pr mice (Halloran, *et al.,* 1988). Just as in the leishmanial disease studied here, CsA treatment in both GVHD and MRL/1pr leads to decreased disease symptoms and immunopathology (Van Bekkum, *et al.,* 1980; Mountz, *et al.,* 1987). The authors also attempted to alter the outcome of infections by treating susceptible mice with intraperitoneal injections of an anti-Ia^d monoclonal antibody (D3137) shown in another investigation (Kurlander and Jones, 1987) to increase resistance toward *Listeria monocytogenes*. No protection was observed, however, when the anti-Ia antibody was given to mice at various times within the first three weeks of infection (data not shown). Indeed, the antibody treatments appeared to have an exacerbating effect when given within the first week of infection. Perhaps the route, dose, and timing of the antibody treatments were inadequate in light of the generalized lymphoproliferative response occurring in the animals.

Evidence collected in this study indicates that early CsA treatment somehow permanently prevents both the development of serious disease and hyper-Ia expression in infected susceptible mice. Indeed, the two phenomenon seem inextricably linked. Whether or not the inhibition of Ia expression by CsA is indeed the cause, or simply a result, of enhanced resistance in the Balb/c mice is unclear. There does appear, however, to be a correlation between an early, sustained level of peritoneal macrophage Ia expression accompanied with a generalized defect in phagocytic activity and the development of severe, progressive murine leishmaniasis.

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STATUS OF THE EASTERN MASSASAUGA, *SISTRURUS C. CATENATUS*, IN INDIANA WITH MANAGEMENT RECOMMENDATIONS FOR RECOVERY

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ABSTRACT: The eastern massasauga, *Sistrurus catenatus catenatus*, is a small rattlesnake currently listed as Endangered in Indiana and as a Candidate Species for listing as Threatened by the U.S. Fish and Wildlife Service. The status of massasauga populations in Indiana was examined to determine the species' past and present distribution, to evaluate threats to extant populations, and to provide recommendations for monitoring, protecting, and enhancing populations. The eastern massasauga was once widely distributed across northern Indiana and relatively abundant in certain localities. The rattlesnake's current range only extends half as far south as it did historically, and most viable populations are restricted to the extreme northeastern corner of the State. Current threats to its existence appear to be largely the same as the historic ones, with habitat loss still being the most critical. While outright habitat loss continues to be a problem, land management practices that allow plant succession may be of equal or greater concern. The most significant threat may be the stabilization of water levels within watersheds and the subsequent loss of the open canopy habitats that the snakes frequent.

KEYWORDS: Conservation, land management, massasauga, *Sistrurus catenatus catenatus,* snake.

INTRODUCTION

The massasauga, *Sistrurus catenatus*, is a small rattlesnake most closely related to the pygmy rattlesnake (*Sistrurus miliarius*). The eastern massasauga, *S. c. catenatus*, is found in the Midwestern United States south of the Great Lakes, in restricted, adjacent areas of Canada, and as far east as portions of New York and Pennsylvania (Minton, 1983; Conant and Collins, 1991). The occurrence of the massasauga in the Midwest and further east has been attributed to its expansion during the Wisconsin interglacial period, when it invaded as a prairie species (Cook, 1993).

The massasauga has been reported from well over twenty counties in Indiana, and Minton (1972) suggested a historical range covering much of the northern half of the State. While apparently once abundant, the massasauga now appears to be in serious decline over its entire range. This snake is currently list-

ed as Endangered in Indiana and is a Candidate Species for listing as Threatened by the U.S. Fish and Wildlife Service. A major cause for the decline of many populations has been the loss of habitat. Over the last hundred years, most prairie areas, as well as most wetlands, have been converted to agriculture. Much of the habitat previously occupied by the massasauga is now no longer available. These snakes are also poisonous, and though their small size reduces the relative risk they pose to people, they have been subject to more efforts at eradication than even the average unlucky snake.

In order to evaluate the extent and to document the reasons for the overall decline of the massasauga, a regional effort has been initiated by the U.S. Fish and Wildlife Service in cooperation with state agencies to establish the status and distribution of this snake in the Midwest. With the support of the U.S. Fish and Wildlife Service and the Indiana Department of Natural Resources, the author conducted the Indiana portion of that effort. In this paper, the natural history of the massasauga, its status in Indiana, the historic and existing threats to its populations, and recommendations for enhancing the security of remaining populations will be reviewed.

NATURAL HISTORY OF THE EASTERN MASSASAUGA

Based on habitat associations reported throughout the range of the animal (Minton, 1972; Reinert and Kodrich, 1982; Seigel, 1986; Weatherhead and Prior, 1992), the habitat used by massasaugas appears to be regionally variable and site dependent. However, the preferred habitats generally are the grassy margins of wetlands and open areas such as prairie. In Indiana, massasaugas are found in sedge fens, grassy meadows, and disturbed areas in the early stages of succession. While they may have occupied prairie habitats in the State in the past, little of this habitat remains today. Almost all the Indiana records link the massasauga to wetlands, which might lead one to presume a preference for such areas. However, *S. c. catenatus* tends to avoid permanently wet areas (Wright, 1941), and individuals are never found swimming, as would commonly occur with typical water snakes. Nevertheless, the snakes have been seen perched immediately adjacent to open water on tufts of sedges or grasses (T. Swinford and J. Hampshire, pers. comm.).

The snake's association with wetlands in Indiana is especially interesting, given that massasaugas are not even semi-aquatic. In fact, rattlesnakes as a taxon are generally associated with relatively xeric habitats. The snake's association with wetlands may be related to the vegetative characteristics of such sites, the type of prey available, the elevated water loss rates, or the massasauga's exclusion from preferred habitats (Atkinson and Netting, 1927; Klauber, 1956).

A characteristic common to all the sites where massasaugas persist in Indiana today is a generally open vegetative structure. Over most of their range, massasaugas tend to avoid heavily wooded areas (Wright, 1941; Bielema, 1973; Seigel, 1986), although Weatherhead and Prior (1992) did find them in openings in coniferous forests in Ontario, Canada. Typically, these sites also have a rela-

tively open shrub layer. This vegetative structure, where tree and shrubs are thinly distributed, allows sunlight to strike the underlying vegetation and the ground, providing places for basking. Prey (rodent) densities for the snakes may be enhanced by the successful growth of sedges, grasses, and herbs. In spite of their preference for largely open areas, the massasauga may show a preference for microsites near isolated trees or shrubs within the open area (Bielema, 1973). This choice may be related to the shade provided by the vegetation as well as to the protection afforded from aerial predators.

Rodents such as voles (*Microtus*) and deer mice (*Peromyscus*) are the predominant prey of adult massasaugas (Wright, 1941; Bielema, 1973; Seigel, 1986). Bielema (1973) found that jumping mice (*Zapus hudsonius*) elicited the most active search and pursuit behavior by massasaugas in captivity. He was unable to elicit attacks on anurans or house sparrows (*Passer domesticus*). Seigel (1986) examined the prey preference of 96 snakes and found that of the 22 that had prey in their stomachs, 84% of the prey was rodents, and 16% was snakes. Snake prey was found only in the stomachs of juvenile massasaugas. Keenlyne and Beer (1973) examined the stomach contents of several hundred sacrificed massasaugas and found that 86% of their prey were voles (*Microtus*). The remainder of the prey were other small mammals, snakes, and birds. No amphibians were found. Overall, adults apparently eat only small rodents, while juveniles accept a greater variety of prey, including small snakes. Some older references indicate that anurans were sometimes included in the diet (Atkinson and Netting, 1927; Curran, 1935).

Massasaugas often show seasonal shifts in habitat use. The typical usage pattern is wet prairie and meadow habitats in the spring and fall and higher, drier habitats in the summer (Bielema, 1973; Reinert and Kodrich, 1982; Seigel, 1986). Some populations do not show a seasonal shift in habitat use (Wright, 1941; Maple, 1964). Linked to the spring-fall habitat pattern is the snake's use of crayfish burrows to hibernate (Maple, 1964; Seigel, 1986), which may explain why massasaugas are often discovered immediately adjacent to water in the spring. Summer habitat use with its reliance on higher, drier sites might explain why roadkills peak in August — the snakes are up in elevated sites rather than down near the water.

PAST AND PRESENT DISTRIBUTIONS OF THE MASSASAUGA IN INDIANA

Methods. The historic distribution of the massasauga in Indiana was estimated using the Indiana Department of Natural Resources' Natural Heritage Database, museum records provided by Alan Resetar (Field Museum of Natural History), the publications of Minton (1972) as well as Whitaker and Gammon (1988), and conversations with regional herpetologists, state personnel, and local residents. Over forty sites were visited to assess the extent and quality of the available habitat, to evaluate potential or existing threats, and to search for snakes. The current distribution of massasaugas was estimated using only observations

since 1985 adjusted by the exclusion/inclusion of some sites based on habitat quality. If suitable habitat at a site was known to have been removed, then the population was assumed to be extirpated at that site. On the other hand, where suitable habitat had remained extensive and of high enough quality to retain a population, the massasauga was inferred to be present even if records from the last ten years did not exist. This assumption is reasonable given the secretive nature of these snakes. To discourage the misuse of site information from this report, specific details on most sites are omitted. Table 1 details the species' status in Indiana on a county by county basis, and Figure 1 shows its historical and current distributions in Indiana.

Historical Distribution. Massasaugas were much more abundant in the past and had a wider distribution in Indiana than they do today. Figure 1 depicts their distribution prior to the 1900s based on historical records within Indiana and the surrounding States. The distribution of massasaugas no doubt ran across the entire northern part of the State, but the extent of their range toward the south is not clear. Minton (1972) discounted the Sullivan County record and limited the southern margin of the massasauga's range to northern Hendricks and Marion Counties, a reasonable assumption given the disjunct nature of the species in Indiana. However, the site in Sullivan County is not far from sites, both confirmed and unconfirmed, having massasaugas in Edgar, Clark, and Crawford Counties in Illinois (Beltz, 1992). The massasauga's range may have continued into Indiana as an extension of these populations along the Wabash River, an extension suggested in Figure 1. Further investigation may clarify whether such an inclusion is warranted or suggest more accurate boundaries for the inclusion. In any case, this portion of the range should be viewed as an extension from Illinois rather than as a disjunct southern population, as a map of the Indiana distribution alone might suggest. Another southerly record recently emerged for Jackson County (Indiana Natural Heritage Database, 1986) but remains unconfirmed. This report was discounted based on the lack of confirmation and the site's distance from other records.

Historically, some of the largest massasauga populations appear to have been along the shores of Lake Michigan in the region of the Indiana Dunes National Lakeshore and throughout the Northern Lakes Natural Region (see Homoya, *et al.*, 1985) of northeastern Indiana. The number of massasauga specimens at the Field Museum in Chicago, which were collected from the Dunes area until the 1920s and 1930s, is quite high (A. Resetar, pers. comm.). To some extent, the number of specimens is due to the area's proximity to Chicago and its collectors. However, good habitat was apparently quite extensive at that time. The Northern Lakes Natural Region, as its name implies, has numerous kettle lakes. The area also had extensive, shallow, ephemeral wetlands and associated habitats, but many have now been drained. The availability of these wetlands, not the lakes, accounts for the historical abundance of the massasauga in this area.

Current Distribution. The present distribution is notably more restricted than the historical one (Figure 1). A southern boundary which encloses all but

Table 1. A summary of the status of the eastern massasauga, *Sistrurus c. catenatus*, in Indiana. Data are presented by county showing the year that the species was last reported from that county, the approximate minimum number of remaining locations for the species within the county, the last year that massasaugas were seen there, the source of the information, and the status (based on the best site in the county) and comments on the status for that county.

County	Sites	Year	Source[1]	Status[2] and Comments
Allen	1	1996	BAK	R; disjunct distribution
Carroll	1	1994	BAK	R; disjunct distribution
Cass	0	1963	SAM	X
Delaware	0	1944	SAM	X
Elkhart	2	1995	BAK	R; good habitat remains
Fulton	0	1970	SAM	X
Hamilton	0	NA	SAM	X; no date or location given
Hendricks	0	1887	SAM	X
Jackson	0	1986	INHD	U; well away from other sightings
Jasper	0	NA	SAM	U; suitable habitat present
Kosciusko	3 - 5	1990	INHD	R; may contain stable populations
Lagrange	5 - 10+	1996	JH	S; several robust population structures
Lake	1	1980s	AR	U; one possible population
La Porte	1	1992	AR	Resetar (1993)
Marshall	1	1993	BAK	R; habitat restricted, disturbed, and isolated
Montgomery	0	1957	SAM	X
Newton	0	1988	INHD	U; no suitable habitat
Noble	1	1995	BAK	R; may be more abundant than indicated
Porter	1	1987	AR	R; severe habitat loss via succession
Pulaski	2	1987	BB	R; small habitat fragments remain
Starke	0	1957	SAM	X; habitat eliminated
St. Joseph	1	1993	BAK	R; snakebite case
Steuben	5 - 10+	1996	FJW	S; several robust population structures
Sullivan	0	NA	SAM	X; disputed locality well south of other sites
Wabash	0	1951	INHD	X
Warren	0	NA	SAM	U; Lee Casebere (IDNR) comment to SAM
Wells	0	NA	SAM	X; no recent observations
Whitley	0	NA	SAM	X

[1] Sources: BB = Bill Bean (IDNR); BAK = Bruce A. Kingsbury (observed or confirmed); JH = Jeff Hampshire (Property Manager, Pigeon River Fish and Wildlife Area); INHD = Indiana Natural Heritage Database (to which I deferred when a source was not a professional scientist or biologist); SAM = Sherman A. Minton (Indiana-Purdue University Indianapolis); AR = Alan Resetar (Field Museum of Natural History); FJW = Fred J. Wooley (Pokagon State Park Naturalist).

[2] Status Codes: U = unconfirmed; X = extirpated; R = rare; and S = stable.

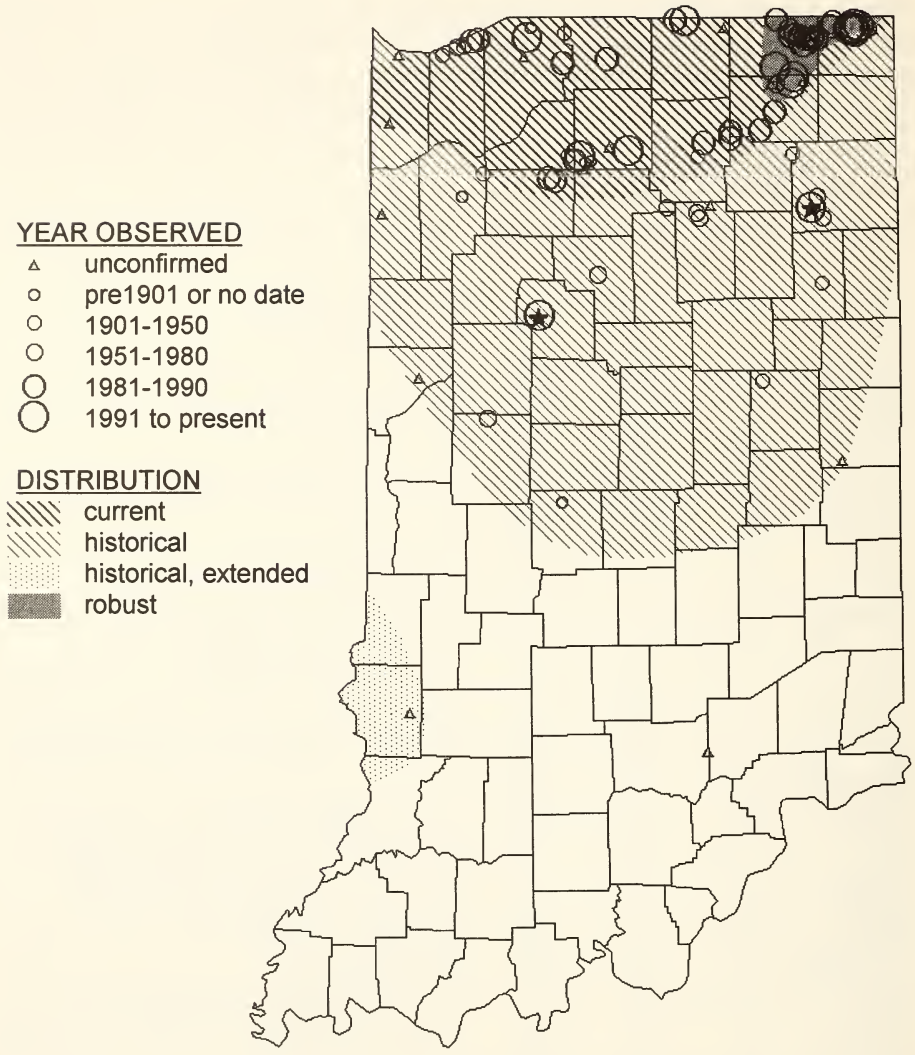

Figure 1. Distribution of the eastern massasauga, *Sistrurus c. catenatus*, in Indiana. The inclusion of the disjunct, southerly region is based on a single, questionable record, which is adjacent to established records in Illinois. Two isolated populations, one in western Carroll County and the other in southwestern Allen County, have been verified as remaining extant and are indicated by stars. Note the restricted size of the area in which most populations remain in the State (shown as the "robust" distribution).

two known populations appears to run only as far south as the northern edge of Cass, Miami, and Wabash Counties. Of the two confirmed populations that lie south of this boundary, the southernmost one is in western Carroll County in a large, but isolated, sedge meadow. The other population is found in southwestern Allen County in a series of moist old fields.

The most dramatic losses in range have occurred to the south and southwest, and most of the western populations have also been extirpated. The loss in range brings up an important point — the simple inspection of a distribution map for the massasauga in Indiana does not provide an accurate assessment of the status of this snake. Looming in the near future is the potential loss of the few remaining western populations in Lake, Porter, and La Porte Counties. Most of the sites in these Counties are small and have been isolated for decades. Succession has removed much of the habitat that has not already been put into agriculture or urbanized. Protecting populations within these Counties will be critical if the current distribution is not to contract even further in the immediate future.

Truly robust massasauga populations are restricted to a small region in the northeastern corner of the State (Figure 1). These populations are relatively large, connected to adjacent populations, and occur in protected habitat. As a result, these populations are at little risk of extirpation for the foreseeable future.

Two of the areas containing massasauga populations are worthy of special attention. The first is Pokagon State Park and its vicinity. This region is by no means uninfluenced by human activity — there are many roads, homes, and farms throughout the area. However, the entire region is interspersed with suitable habitat fragments, many of which are found in areas with protected habitat (e.g., Pokagon State Park and the Marsh Lake Fish and Wildlife Area). Interstate 69 does form an effective barrier just east of the park, but there are several ponds that pass beneath the highway that may allow occasional genetic interchange. The second area is the Pigeon River State Fish and Wildlife Area and the surrounding environs. This area is also interspersed with suitable habitat, much of it protected within the Fish and Wildlife Area. Fens and associated habitats are found along the Pigeon River and several of its tributaries. Many sites have records for massasaugas, including some reports during the time period of this study. Some of the largest suitable habitat fragments in the State are included in this area, and extensive marginal habitat also exists to act as corridors between these fragments.

FACTORS CAUSING THE DECLINE OF THE MASSASAUGA

To evaluate the factors which have led to the decline of massasaugas populations in the past and which may continue to do so in the future, I reviewed the available literature on the species, spoke with herpetologists, other authorities, property managers, and land owners, and visited selected sites. Knowing the factors which threaten massasaugas, recommendations for removing, or at least reducing, the identified threats can be made.

Habitat Loss. Without doubt, the most profound factor leading to the decline of massasaugas has been the conversion of their habitat into farmland. Almost all tillable land in Indiana has been put into agriculture. The prairie habitat is largely gone, and most wetlands have been successfully drained. Habitat loss due to agriculture no doubt continues to some extent, but the loss was more extensive in the past.

Currently, the most critical factor in habitat loss is succession. Massasaugas appear to be ecotonal specialists. The habitats that they use are often transitory in nature, requiring disturbances such as fires and floods to maintain them. The regulation of water levels in wetlands and watersheds has no doubt played a much more significant role in habitat loss than fire suppression. Seasonal variation in wetland water levels keeps an area open by inhibiting the encroachment of species such as cattails on the hydric side of the ecotone and brush and trees on the terrestrial side. Habitat losses due to succession are more extensive than might initially be realized, because the hydrology of entire areas is simultaneously impacted. Inspection of numerous lake complexes in northern Indiana reveals that miles of watershed may have virtually the same elevation and that shifts of less than a meter in water depth would dramatically change the shoreline over vast areas. Historically, seasonal flooding did just that—each year, many square miles of habitat might be flooded by shallow water. The flooding would also have a high degree of unpredictability. The result of flooding would be the maintenance of vast tracts of ephemeral wetlands, that are all but gone in northern Indiana. They have been converted to farmland, or, along channelized river banks, succeeded by forest.

Malicious Killing. Another problem for massasaugas is outright killing. Snakes as a taxon are unreasonably persecuted, and things are worse for massasaugas because they are venomous. Their killing is unfortunate, because, in addition to any moral or ethical notion that they have a right to co-exist with us, they are useful for rodent control. In addition, as poisonous animals are concerned, massasaugas are relatively non-threatening. Finally, most of them live in areas that relatively few people enter, and they rely on crypsis to avoid detection. They may live in an area for years without anyone knowing that they are there.

Even when encountered, massasaugas prefer not to bite. In my encounters with them, I have never observed the snakes to strike. Instead, the snakes try to remain undetected. When they are detected, they try to flee. Prior and Weatherhead (1994) evaluated the defensive behavior of massasaugas. These researchers either (1) stepped next to (within 0.5 m) and then continued on, (2) stopped for 30 seconds next to, or (3) stepped over massasaugas they knew were present (they were monitoring them with radiotelemetry). The snakes remained motionless 58% to 66% of the time, depending on the treatment; of those that responded in some way, 66% rattled and fled, while the rest simply rattled. Out of 174 trials using 21 snakes, no strikes were ever observed! In another study (appar-

ently on the same population), Hedgecock (1992) presumably stepped on the snakes; that is, the foot was actually placed on top of the snake, although it goes unstated. Only 7% of the snakes that were "stepped upon" in the study struck at the investigator's foot!

While massasaugas are venomous enough to warrant respect, their small size limits the dose that they can deliver. Even without recent medical advances, the bite of this snake has rarely proven to be fatal. Wright (1941) reviewed 24 cases of snakebite, with and without the availability of antivenin, and no fatalities were observed. Minton (1972) did mention that some fatalities had occurred. Generally, their bites result in regional inflammation and discomfort. Being bitten by them is thus not a trivial event.

Incidental mortality may be quite significant. Many locality records come as the result of roadkills. In Indiana, massasaugas are most mobile in August and are most susceptible to traffic at that time. Unfortunately, many of these casualties are gravid females. Agriculture also takes its share of these snakes. The tilling of fields, especially fallow fields where the snakes have taken up residence from neighboring areas, kills the snakes living there. Harvesting and baling feed crops also leads to fatalities. The author has listened to many stories about massasaugas being found not only under bales but in them as well!

A final problem for massasaugas is that they are sought out by some collectors. Because massasaugas are venomous, they are perceived by hobbyists as "exotic" or novel. Ineffectual State protective laws also minimize the legal risk of collecting. One factor which will help the massasauga at most sites is the fact that they are so hard to find. This reduces the attraction for many illegal collectors, as it takes too much time to find them for it to be profitable.

State and Federal Status of the Massasauga. The classification of the eastern massasauga as Endangered by Indiana and Threatened by the U.S. Fish and Wildlife Service is appropriate. The snake should not be Federally listed as Endangered, since it is not in imminent danger of being completely extirpated, either in this State or over its entire range. Indiana does not legally distinguish between Threatened and Endangered (C. Gremillion-Smith, Indiana Department of Natural Resources, pers. comm.). Thus, although the species is not in immediate peril of extirpation in the State, the massasauga is listed as Endangered here. The species has suffered a severe contraction in range in this State and others, and further losses are likely in the near future. Listing is thus appropriate, and massasaugas should be afforded a high priority when management decisions are being made in areas where they are suspected to occur.

MANAGEMENT RECOMMENDATIONS

While we might hope that sites containing massasaugas will be left undisturbed, this will not often be the case. Many populations reside on private property or in areas managed for other species, such as waterfowl. Given that most of the land on which these animals live is used in some way, land uses

which are compatible with population persistence should be promoted. Such activities may remove individuals, but they are less likely to threaten the existence of the entire population.

In those cases where managing habitat for massasaugas is an option, the following recommendations should be considered:

1. Habitat maintenance should be geared towards maintaining open habitat, especially at sites where there is some seasonal saturation of the soil, through burning, mowing, or selective herbicidal applications. However, a number of risks to the massasaugas are associated with all of these practices. Seigel (1986) noted the loss of individuals during burning, and Wright (1941) and various property managers noted losses during mowing. No doubt herbicides have their side effects as well. Many of the problems with habitat management can be mollified by correctly timing the practice to minimize losses—massasaugas are largely inactive prior to late April and after September. They also tend to stay underground on cold, overcast days. Perhaps crops could be harvested later in the year in areas occupied by massasaugas.
2. Permit natural water level fluctuations. Controlling water in impoundments is common in fish and wildlife areas and other managed situations. Maintenance at fixed levels leads to losses of suitable habitat (see above). Land managers are often concerned with keeping habitat open, and fluctuating water levels may promote such habitat.
3. Promote the development of safe, useable corridors. Providing safe corridors between adjacent habitat fragments enhances the usefulness of both fragments to the snakes. Land managers should keep this in mind when planning land use in a habitat mosaic. Some areas of human disturbance may act as corridors, if not actual habitat. For example, highway right-of-ways are essentially maintained as grassland, and they often have ephemerally wet areas. These right-of-ways often border habitat fragments which are suitable massasauga habitat. As such, they can act as linkages and as supplemental habitat, especially if the grasses growing there are suitable forage for rodents. The margins of railroad beds, bikeways, and local roadways may also act in the same way. Maximizing the benefits of such thoroughfares for massasaugas will preclude mowing the entire right-of-way during the activity season (the strip bordering the road could be mowed all year).
4. The public should be educated about the ecological role of the snake and the low risk that it imposes on people. Clarifying the snake's role will undoubtedly aid in its acceptance. Protecting any snake is challenging, given the common fear of such animals. Protection of a poisonous and potentially harmful animal is even more difficult. If people learn that, unless actually picked up, massasaugas pose little risk to them, perhaps they can be convinced to leave the massasauga alone.

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FISHES OF THE INLAND WATERS OF BEAVER ISLAND, CHARLEVOIX COUNTY, MICHIGAN

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ABSTRACT: The shallow water fishes of eleven inland water bodies on Beaver Island, Charlevoix County, Michigan, were surveyed during the summer of 1994 using seines, traps, and standard fishing techniques. This information was supplemented with historic data and reports by the Michigan Department of Natural Resources, other unpublished studies, reports by residents of the island, and specimens housed in the Natural History Museum of the Central Michigan University Biological Station. The result is the first comprehensive list of the fish fauna of Beaver Island. A total of 33 species and one subspecies, representing 11 families, was noted for the island. Seven of these reports are new records. The collection of *Gasterosteus aculeatus* suggests that the range of this species in the Great Lakes drainage is expanding westward, as its western limit had been previously reported as Lake Ontario. Notes on the history as well as habitat descriptions of each collection site on the island are included.

KEYWORDS: Beaver Island, fish, *Gasterosteus aculeatus*, Lake Michigan.

INTRODUCTION

The first known settlement on Beaver Island (French explorers) pre-dated the arrival of the Pilgrims in North America. In 1847, the island was controlled by a Mormon monarchy with 2,000 inhabitants, and in 1856, the assassination of the king of the island triggered a hostile takeover by mainland Irish immigrants. Currently, about 400 permanent residents live on the island, and their main sources of income are fishing, logging, and tourism. Unlike some of the other islands in the Great Lakes (e.g., Mackinac and Drummond Islands), Beaver Island has maintained its natural character. However, in recent years, increased tourism, the development of second homes in previously undeveloped areas, sport fishing pressure, and the potential threats of introduced and exotic species have justified efforts to document the island's pre-disturbance biota and ecology.

Since the establishment of the Central Michigan University Biological Station on Beaver Island in 1964, faculty, students, and visiting scientists have worked hard to inventory and study the island's native flora and fauna. However, most of these studies have focused on the herpetofauna and aquatic vascular plants (J.C. Gillingham and D.E. Wujek, pers. comm.).

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The first survey of the fishes of Beaver Island's inland waters was conducted by the Michigan Department of Natural Resources (unpubl. rep., 1960). Additional unpublished accounts were prepared in the late 1960s (e.g., F. Menapace, 1966; R.D. Simpson, 1967; R. Mellon, 1968; B. Foster, 1969). Most of these reports are restricted to the larger lakes. Few investigators have surveyed the smaller bog lakes, and none have reported on the lotic systems or beach ponds and pools. The objective of this study, then, was to provide baseline information about the diversity and history of the fishes of Beaver Island for use by future investigators.

STUDY AREA

Beaver Island is located in Lake Michigan, 48 km northwest of Charlevoix, Michigan (Figure 1). It is the largest of seven islands in the archipelago, having an area of approximately 137 square kilometers. The islands are of glacial origin, having a substrate made up almost exclusively of till or outwash. The dominant natural forest cover is beech-maple with red and white pine as subdominants. The southern portion of the island is covered with dense cedar swamps and bogs. Much of this area occurs within the Pigeon River State Forest.

Seven lakes or ponds occur on the island (Figure 1): Barney's Lake (20 ha), Egg Lake (14 ha), Font Lake (173 ha), Fox Lake (34 ha), Green's Lake (30 ha), Lake Geneserath (222 ha), and Miller's Marsh (5 ha). An eighth, Round Lake (4 ha), is ephemeral and, in recent years, mostly dry. Egg, Fox, and Green's Lakes are *Sphagnum*-bog lakes, while Barney's Lake is surrounded by a circumneutral fen (Fitzgerald and Bailey, 1975). Font Lake also harbors minerotrophic peat communities. Limnological data for five of the island's lakes are presented in Table 1 (K. Ginn, unpubl. student rep., 1994).

Two lotic systems, Iron Ore Creek and Jordan River, occur on the island (Figure 1). Jordan River is relatively permanent, while Iron Ore Creek is usually seasonal. Both support gravel as well as muck substrata.

MATERIALS AND METHODS

The shallow waters of eleven water bodies on Beaver Island (Figure 1) were surveyed; seven were lakes or large ponds (Barney's, Egg, Font, Fox, Geneserath, and Green's Lakes and Miller's Marsh), two were lotic systems (Jordan River and Iron Ore Creek), and two sites included beach pools and ponds (Sucker Point and Big Sandy Bay). A 4-meter long seine was used to survey fishes in each of the sampling areas. Seining was conducted several times during the morning and evening hours in the littoral benches of each lake and along entire stretches of the creek and river. In addition to seining, small traps, baited with liver, were placed in various habitats at each site and checked daily for a period of one week. Standard sport fishing techniques (involving approximately 30 hours) were used to capture species of deeper waters. Collections were conducted throughout the summer of 1994, and voucher specimens are held in the Natural History Museum of the Central Michigan University Biological Station.

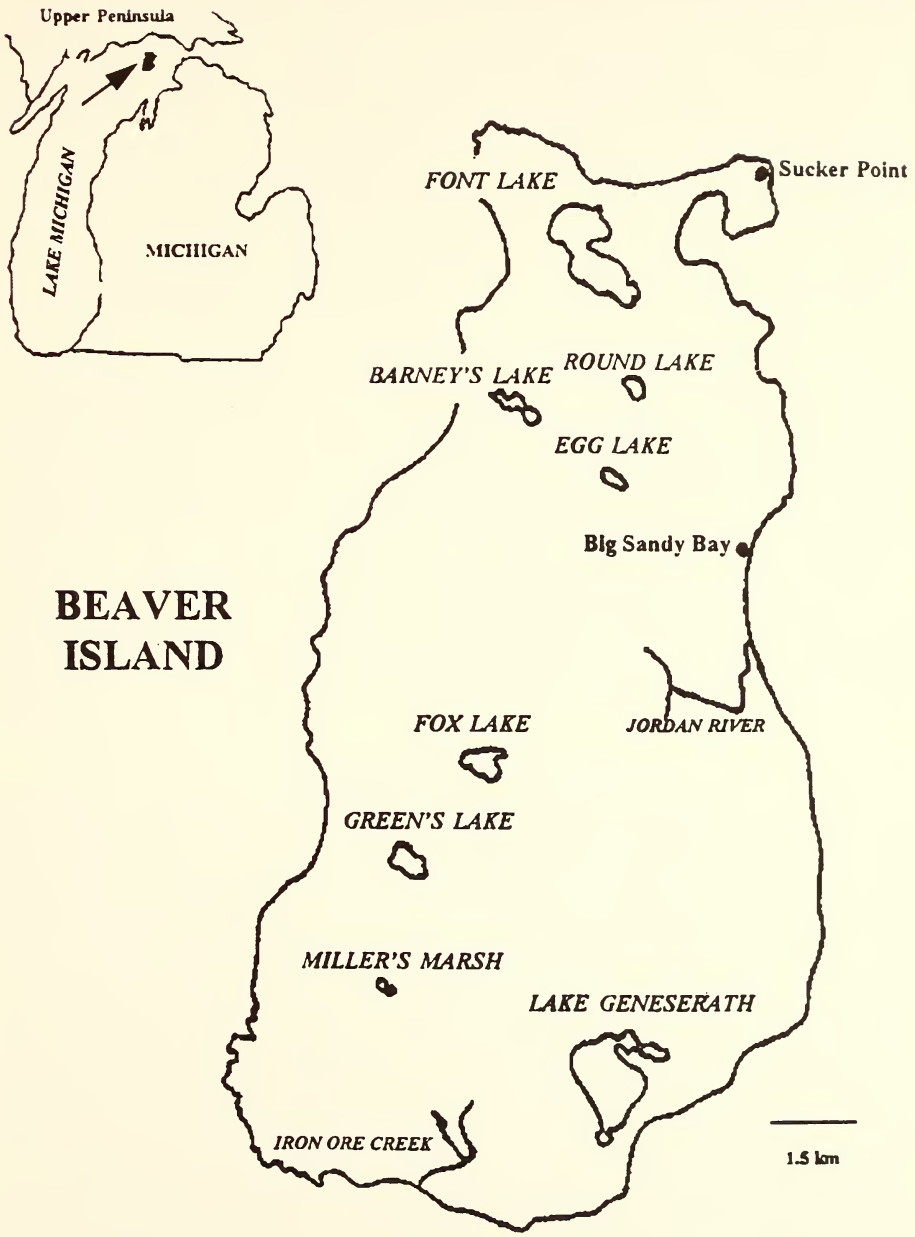
Upper Peninsula
LAKE MICHIGAN
MICHIGAN
FONT LAKE
Sucker Point
BARNEY'S LAKE
ROUND LAKE
EGG LAKE
Big Sandy Bay
BEAVER ISLAND
FOX LAKE
JORDAN RIVER
GREEN'S LAKE
MILLER'S MARSH
LAKE GENESERATH
IRON ORE CREEK
1.5 km

Figure 1.

Table 1. Limnological variables from several lakes on Beaver Island.

	Barney's Lake	Egg Lake	Font Lake	Fox Lake	Lake Geneserath
Maximum depth (m)	3.7	—	2.5	5.3	15.6
O_2 (mg/l)	9.02	—	8.61	8.58	8.28
$CaCO_3$ (mg/l)	110	—	62.4	5.70	86.6
pH	8.88	9.0	8.5	6.74	8.38
Temp (° C on August 2)	24.5	—	24.0	21.4	21.6

The species list resulting from collections conducted during 1994 was supplemented with reports from other sources. The archives and natural history collection of the Central Michigan University Biological Station were checked, and all relevant material (including unpublished student papers as well as reports by the Michigan Department of Natural Resources) were reviewed. These sources are available upon request from J.C. Gillingham at the Department of Biology, Central Michigan University.

Age determination of the perch taken from Green's Lake was conducted by removing and analyzing several non-regenerated scales from the area just behind the pectoral fin of each fish. The age for each specimen was recorded as the number of annual "plates" per scale.

RESULTS AND DISCUSSION

A total of 33 species and one subspecies of fish, representing 11 families, were documented as occurring or having occurred on the island since 1942 (Table 2). Two species (*Onchorhynchus mykiss* and *Salvelinus fontinalis*) no longer occur on the island, one (*Esox masquinongy* x *lucius*) is an introduced hybrid, and one (*Cyprinus carpio*) is an introduced exotic. Reports of *Ammocrypta pellucida* and *Etheostoma caeruleum* (F. Menapace, unpubl. student rep., 1966) were not recognized due to range limitations, the absence of voucher specimens, and the inability to locate living specimens. *Esox masquinongy* x *lucius*, *Cyprinus carpio*, *Phoxinus eos*, *Catostomus catostomus*, *Fundulus diaphanus* ssp. *menona*, *Gasterosteus aculeatus*, and *Cottus bairdi* are new records for the island. Unidentified members of the genera *Notropis* and *Moxostoma* were also recorded.

The Cyprinidae, Centrarchidae, and Percidae had the largest representation (6 species each; Table 1). The most frequently encountered and widely distributed species were *Esox lucius* (northern pike), *Culaea inconstans* (brook stickleback), *Lepomis macrochirus* (bluegill sunfish), and *Perca flavescens* (yellow perch). Ten species were reported from only a single site. Several of these have likely been extirpated due to unfavorable habitat.

Barney's Lake. Eleven species, including three new records, were reported for Barney's Lake. The presence of *Fundulus d. diaphanus* (banded killifish) in this lake as well as in another land-locked lake (Font Lake) is curious, as waters associated with Lake Michigan (Big Sandy Bay and Sucker Point) harbor *Fun-*

dulus d. menona. This dichotomous distribution may be an artifact of the island's previous attachment to the mainland.

The 1960 report of *Micropterus dolomieui* (smallmouth black bass) by the Michigan Department of Natural Resources probably represents stocked fish. The current habitat at Barney's Lake (mud-bottom) and the lack of recent reports suggest that this species no longer occurs there. Recent reports of this species, with the exception of those from coastal ponds, are lacking from the island's inland waters. Reports of black bass from the island have been almost entirely restricted to *Micropterus salmoides* (largemouth black bass) in recent years. This species is most common in warm, eutrophic, muddy waters, such as those provided by most of Beaver Island's lakes.

Egg Lake. A single species, *Culaea inconstans*, was noted in this shallow bog lake. While the interstitial waters of the bog mat have pH values of 3.5, the open water of the lake has values as high as 9.0. The apparent lack of a rich assemblage of fish may be a function of water depth, because a "false bottom" of flocculent organic sediments is no more than one meter from the surface in most places. The entire water column is trophogenic, and during peak summer months, low dissolved oxygen concentrations are probably limiting.

Font Lake. Eleven species were reported for this lake. The report of *Esox masquinongy* x *lucius* (tiger muskellunge) was from a local fisherman, who caught an individual during the summer of 1994. The specimen was the tiger variety, a stocked hybrid.

The reports of *Ammocrypta pellucida* (eastern sand darter) and *Etheostoma caeruleum* (rainbow darter) by F. Menapace (unpubl. student rep., 1966) are probably incorrect. Beaver Island is north of the natural range of both species (Page and Burr, 1991). The reported specimens were probably *Etheostoma nigrum* (johnny darter) and *Etheostoma exile* (Iowa darter). These species are somewhat similar to *A. pellucida* and *E. caeruleum*, respectively, and the presence of the latter two has been verified by voucher specimens.

Fox Lake. Since 1960, twelve species have been reported from Fox Lake. The Michigan Department of Natural Resources poisoned Fox Lake during the summer of 1961, presumably killing most or all of the fish. In the fall of 1961 and in 1962, the Michigan Department of Natural Resources stocked *Salvelinus fontinalis* measuring nine inches in length. *Oncorhynchus mykiss* (rainbow trout; stocked by the Michigan Department of Natural Resources in 1964) and *Salvelinus fontinalis* are certainly extirpated at present, as the habitat is not conducive to their reproduction, and stocking has not occurred for several decades. No reports of these species are known after 1964.

Micropterus dolomieui was reported by the Michigan Department of Natural Resources in 1960; however, no reports are known since then. Most current records are of *M. salmoides*. Reports of *M. dolomieui* in the inland lakes may have resulted from stocked fish which no longer exist.

Green's Lake. Whether Green's Lake, a dystrophic bog lake, ever supported naturally occurring fish populations is not known. The Michigan Department of

Table 2. The fishes reported from the inland waters of Beaver Island, Michigan (Michigan Department of Natural Resources, 1942; Michigan Department of Natural Resources, 1960; Michigan Department of Natural Resources, 1964; Menapace, 1966; Simpson, 1967; Mellon, 1968; anonymous, 1969; anonymous, 1972; anonymous, 1994). These sources have not been published and are available from J.C. Gillingham of Central Michigan University. The species in bold-face print represent new records.

	Site[a]									
	1	2	3	4	5	6	7	8	9	10
SALMONIDAE										
Oncorhynchus mykiss				1964[b]						
Salvelinus fontinalis					1960			X[c]		
UMBRIDAE										
Umbra limi			1960	X				X	X	
ESOCIDAE										
Esox lucius	X			X	1972	1960		X		
Esox masquinongy* x *lucius			1994							
CYPRINIDAE										
Cyprinus carpio									X	X
Notemigonus chrysoleucus				1960					X	X
Notropis heterolepis		1960		1966, 1967[b]						
Notropis sp. 1										X
Notropis sp. 2										X
Phoxinus eos									X	X
Pimephales notatus						1960				
CATOSTOMIDAE										
Catostomus catostomus								X		
Catostomus commersoni			1960, 1966, X			1960, 1968[b]		X	X	
Moxostoma sp.								X		
ICTALURIDAE										
Ictalurus melas					1942,	1969				
Ictalurus nebulosus	1960				X	1960				

	Sites[a]									
	1	2	3	4	5	6	7	8	9	10
CYPRINODONTIDAE										
Fundulus diaphanus diaphanus		1960, X		1960, 1966						
Fundulus diaphanus menona									X	X
GASTEROSTEIDAE										
Culaea inconstans		X	1960					X	X	X
Gasterosteus aculeatus									X	X
COTTIDAE										
Cottus bairdi							X			
CENTRARCHIDAE										
Ambloplites rupestris		X			X		1969[b], X			X
Lepomis gibbosis				1960		X				
Lepomis macrochirus	X		1968	1960	1942	X				
Micropterus dolomieui	1960			1960						X
Micropterus salmoides	1960			X		X				
Pomoxis nigromaculatus				1960						
PERCIDAE										
Ammocrypta pellucida			1966							
Etheostoma caeruleum			1966							
Etheostoma exile	1960					1960				
Etheostoma nigrum	1960		1960, 1966			1960				
Percina caprodes						1960				
Perca flavescens	1960		1960, 1967[b]	1960, X	X	X				

[a] Sites: 1 = Barney's Lake; 2 = Egg Lake; 3 = Font Lake; 4 = Fox Lake; 5 = Green's Lake; 6 = Lake Geneserath; 7 = Iron Ore Creek; 8 = Jordan River; 9 = Sandy Bay Ponds and Pools; 10 = Sucker Point Ponds and Pools.

[b] Specimen in the Central Michigan University Biological Station collection.

[c] An X identifies a species collected in 1994; a voucher specimen was placed in the Central Michigan University Biological Station collection.

Natural Resources (unpubl. rep., 1942) reports stocking fish into the lake as early as 1942. During that year, both *Ameiurus melas* (black bullhead) and *Lepomis macrochirus* were introduced. No other fishes were noted by the Michigan Department of Natural Resources. Later, in 1972, several *Esox lucius* were netted from Barney's Lake and introduced into Green's Lake (anonymous source). The number of introductions and the success of the endeavor are unknown.

Residents of the island reported that at one time, presumably in the early seventies, a population of *Perca flavescens* existed in the lake. Some individuals were reported as being more than 40 cm in length. The residents believed that a winter freeze in the late seventies or early eighties killed all of the fish in the lake. However, collections during the summer of 1994 confirmed the continued existence of *P. flavescens* in the lake. The mean length of captured specimens was 13.8 cm with a range of 13.6 to 15.3 cm. Analysis of growth patterns on the scales taken from the fish showed that they ranged in age from 5 to 7 years (mean = 5.75 yrs). Whether the original population and/or the existing population represent naturally occurring fish or fish that were introduced by island residents is not known.

The only species, other than *P. flavescens*, that was collected in 1994 was *Ameiurus melas*. These fish are apparently descendants of the 1942 stocking. *Lepomis macrochirus* introductions into Green's Lake were apparently unsuccessful, as no specimens were found to exist there.

Lake Geneserath. Thirteen species were reported from this lake, the most for any of the sites studied. The lake is the only site on the island where *Percina caprodes* (logperch) has been reported. Sport fishing pressure on this lake is probably greater than anywhere else on the island. Recently, residents have discussed the merits of stocking *Stizostedion vitreum* (walleye) into the lake. This lake is the only lake on the island considered to be deep enough to provide sufficient habitat for this species.

Iron Ore Creek. This lotic system is rather ephemeral, depending on the amount of rainfall in a given year. The two species noted, *Oncorhynchus mykiss* and *Cottus bairdi* (mottled sculpin), are migrants from Lake Michigan.

Jordan River. Like Iron Ore Creek, the fishes in Jordan River, for the most part, are transient species from Lake Michigan. Suckers, *Catostomus catostomus* (longnose sucker) and *C. commersoni* (white sucker), are found only in the spring during their spawning run. *Moxostoma* sp. (redhorse sucker) has been reported (J.C. Gillingham, pers. comm.), but no voucher specimens have been located. Only *Umbra limi* (central mudminnow) and *Culaea inconstans* appear to be permanent residents of the river. A single juvenile of *Esox lucius* was also noted.

Sandy Bay Ponds and Pools. Several discrete ponds were surveyed on Big Sandy Bay. A total of eight species was noted. Many appeared to be transients from coastal waters. *Umbra limi* and *Culaea inconstans* are permanent residents and breed in the algal mats and submergent macrophytes. The presence of *Gasterosteus aculeatus* (three-spined stickleback) at both the Sandy Bay and the

Sucker Point stations suggests that this species is expanding its western range within the Great Lakes drainage, as Page and Burr (1991) report the species' westernmost occurrence in the Great Lakes drainage as Lake Ontario.

Sucker Point Ponds and Pools. Like Big Sandy Bay, most of the ten species found here are washed-in on an annual basis from Lake Michigan and become stranded in the pools. Although the ponds are comparatively large and deep (1 m), it is unlikely that they are deep enough to support large fish such as *Cyprinus carpio* (carp) throughout the winter.

CONCLUSION

The fish fauna of Beaver Island's inland waters is somewhat similar in overall species composition and abundance to corresponding habitats in other parts of northern Michigan. However, non-game predators such as gar and bowfin are curiously absent. In addition, the Cyprinidae are relatively poorly represented. More intensive sampling and taxonomic research is needed to ascertain their actual richness and abundance. Small, non-game forage species such as cyprinids are often better indicators of environmental quality.

Although the results of the present study probably represent the majority of Beaver Island's fishes, additional sites and collecting techniques should be explored. Several beaver ponds remain unsampled, and identifications of specimens known only by genus are needed.

As sport fishing pressure increases with tourism, quantification and age analysis of gamefish populations may be needed for management purposes.

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AN UPDATED CHECKLIST OF INDIANA DRAGONFLIES (ODONATA: ANISOPTERA)

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ABSTRACT: Published reports of Indiana Odonata appeared more or less regularly from the turn of the century until 1971. Two workers, E.B. Williamson and B.E. Montgomery, were largely responsible for this work, and between them, they reported 100 species of dragonflies (Anisoptera) for Indiana. Williamson published an annotated list of Indiana Odonata in 1917 in which he gave each species a number from 1 to 125. As new species were reported, they were added to the list at the appropriate taxonomic position by adding an a, b, c, and so on to an existing number. Since 1971, no additional published reports have appeared, and changes in classification and nomenclature make an update of the State list of dragonflies necessary. Williamson's numbering system does not fit well with the changes that have occurred, and the author recommends that it be dropped in favor of a more up-to-date listing. Several species reported for the State are no longer recognized, and one species new to Indiana has recently been recorded. Currently, 98 species of dragonflies are recorded for Indiana.

KEYWORDS: Anisoptera, Indiana dragonflies, Indiana records, Odonata.

INTRODUCTION

Systematic surveys of Indiana Odonata, conducted almost annually from the turn of the century by Williamson, Montgomery, and others, ceased in the late 1960s. The surveys were resumed four years ago by the author with the intent to update State records and to develop a field guide to the common species in the State.

The first comprehensive report on the Odonata of Indiana was published by E.B. Williamson (1900a). The report included keys and short descriptions for 84 species of adult and larval damselflies (Zygoptera) and dragonflies (Anisoptera) which had been recorded in the State up until that time. Williamson (1900b, 1901) added to the list in 1900 and 1901, and he published an annotated list of Indiana's Odonata in 1917. In this latter paper, he listed by number 44 species of damselflies and 81 species of dragonflies. The dragonflies were numbered 45-125 and grouped by suborder, family, genus, and species. In a paper published in 1921, Williamson added one new species of dragonfly to the State list. In order to keep the 1917 numbering system intact, he began the practice of adding new species to the list in the appropriate taxonomic position by adding a lower case letter to a previously existing number. Thus, the first addition to the State list, *Gomphus viridifrons* Hines, became number 66a. Although the list con-

tinued to grow with the passing years, the dragonflies continued to be numbered from 45 to 125, and the species listed in the 1917 paper retained their original numbers.

In the early 1920s, Williamson recruited a young public school teacher named B. Elwood Montgomery to help him with his work. Montgomery's first paper on Indiana dragonflies was published in 1925. Using his own records as well as notes given him by Williamson, he added three species of gomphids to the State list, using the designations 52a, 59a, and 59b. These new records raised the total number of dragonflies (Anisoptera) to 85. Additional papers appeared in 1926, 1928, 1929, 1931, and 1932. These papers discussed the new species that had been collected during those years.

Following Williamson's death in 1933, Montgomery completed a Ph.D. degree and took a position at Purdue University, where he stayed for the remainder of his career. He carried on the work begun by Williamson and continued to publish new records on Indiana Odonata (1934, 1935, 1937, 1941, 1951, 1953, 1955, 1967, 1971). By the time of his death in 1983, Montgomery had increased the list of Indiana species of Anisoptera to 100.

A number of changes have been made in the scientific names and classification of the Anisoptera in recent years, making an update necessary. One species new to Indiana has been recorded since Montgomery's 1971 paper, bringing the updated list of species reported for Indiana to 98. The new species is indicated below with an asterisk. The numbers in parentheses at the left of each species refer to Williamson's old numbering system. Those wishing an updated list of species using the old numbering system need only rearrange the numbers in proper numerical order. The listing used in this paper follows the order of other recently published State lists (Glotzhober, 1995; Tennessen, *et al.*, 1995; Miller and Gustafson, 1996; May and Carle, 1996).

DRAGONFLIES (ODONATA:ANISOPTERA) OF INDIANA

Petaluridae (Petaltails)

(45) *Tachopteryx thoreyi* (Hagen, 1858)

Aeshnidae (Darners)

(73) *Aeshna canadensis* Walker, 1908
(74) *Aeshna clepsydra* Say, 1839
(75) *Aeshna constricta* Say, 1839
(76) *Aeshna mutata* Hagen, 1861
(77) *Aeshna tuberculifera* Walker, 1908
(78) *Aeshna umbrosa* Walker, 1908
(79) *Aeshna verticalis* Hagen, 1861
(72) *Anax junius* (Drury, 1770)
(72a) *Anax longipes* Hagen, 1861

(71) *Basiaeschna janata* Say, 1839
(70) *Boyeria vinosa* (Say, 1839)
(81) *Epiaeschna heros* (Fabricius, 1798)
(80) *Nasiaeschna pentacantha* (Rambur, 1842)

Gomphidae (Clubtails)

(52b) *Arigomphus cornutus* (Tough, 1900)
(57) *Arigomphus furcifer* (Hagen, 1878)
(62a) *Arigomphus lentulus* (Needham, 1902)
(63) *Arigomphus submedianus* (Williamson, 1914)
(66) *Arigomphus villosipes* (Selys, 1854)
(68) *Dromogomphus spinosus* Selys, 1854
(69) *Dromogomphus spoliatus* (Hagen, 1858)
(52) *Erpetogomphus designatus* Hagen, 1858
(53) *Gomphurus crassus* Hagen, 1878
(55a) *Gomphurus externus* Hagen, 1858
(56) *Gomphurus fraternus* (Say, 1839)
(54) *Gomphurus lineatifrons* Calvert, 1921
(64) *Gomphurus vastus* Walsh, 1862
(65) *Gomphurus ventricosus* Walsh, 1863
(55) *Gomphus exilis* Selys, 1854
(58) *Gomphus graslinellus* Walsh, 1862
(59) *Gomphus lividus* Selys, 1854
(60) *Gomphus quadricolor* Walsh, 1863
(61) *Gomphus spicatus* Hagen, 1854
(66a) *Gomphus viridifrons* Hine, 1901
(50) *Hagenius brevistylus* Selys, 1854
(51) *Ophiogomphus rupinsulensis* (Walsh, 1862)
(49) *Progomphus obscurus* (Rambur, 1842)
(52a) *Stylurus amnicola* (Walsh, 1862)
(58a) *Stylurus laurae* (Williamson, 1932)
(59a) *Stylurus notatus* (Rambur, 1842)
(59b) *Stylurus plagiatus* (Selys, 1854)
Stylurus scudderi (Selys, 1873)
(62) *Stylurus spiniceps* (Walsh, 1862)

Cordulegastridae (Spiketails)

(46) *Cordulegaster diastatops* (Selys, 1854)
Cordulegaster bilineata Carle, 1983
(46a) *Cordulegaster erronea* Hagen, 1878
(47) *Cordulegaster maculata* Selys, 1854
(48) *Cordulegaster obliqua* (Say, 1839)

Macromiidae (Cruisers)

(82) *Didymops transversa* (Say, 1839)
(83) *Macromia illinoiensis* Walsh, 1862
(84) *Macromia pacifica* Hagen, 1861
(85) *Macromia taeniolata* Rambur, 1842
(86) *Macromia wabashensis* Williamson, 1909

Corduliidae (Emeralds)

(92) *Dorocordulia libera* (Selys, 1871)
(89) *Epitheca cynosura* (Say, 1839)
(87) *Epitheca princeps* Hagen, 1861
(91) *Epitheca spinigera* (Selys, 1871)
(88) *Neurocordulia obsoleta* (Say, 1839)
(88a) *Neurocordulia yamaskanensis* (Provancher, 1875)
(93) *Somatochlora ensignera* Martin, 1906
(93a) *Somatochlora hineana* Williamson, 1931
(94) *Somatochlora linearis* (Hagen, 1861)
(95) *Somatochlora tenebrosa* (Say, 1839)

Libellulidae (Skimmers)

(118) *Celithemis elisa* (Hagen, 1861)
(119) *Celithemis eponina* (Drury, 1773)
(119a) *Celithemis fasciata* Kirby, 1889
(120a) *Celithemis verna* Pritchard, 1935
(107) *Erythemis simplicicollis* (Say, 1839)
(106a) *Erythrodiplax minuscula* (Rambur, 1842)
(106b) *Erythrodiplax umbrata* (Linnaeus, 1758)
(116) *Leucorrhinia frigida* Hagen, 1890
(117) *Leucorrhinia intacta* Hagen, 1861
(96) *Libellula cyanea* Fabricius, 1775
(96a) *Libellula deplanata* Rambur, 1842
(98) *Libellula incesta* Hagen, 1861
(97) *Libellula julia* (Uhler, 1857)
(99) *Libellula luctuosa* Burmeister, 1839
(104) *Libellula lydia* Drury, 1770
(100) *Libellula pulchella* Drury, 1770
(101) *Libellula quadrimaculata* Linnaeus, 1758
(102) *Libellula semifasciata* Burmeister, 1839
(103) *Libellula vibrans* Fabricius, 1793
(106) *Nannothemis bella* (Uhler, 1857)
(115) *Pachydiplax longipennis* (Burmeister, 1839)
(121) *Pantala flavescens* (Fabricius, 1798)
(122) *Pantala hymenaea* (Say, 1839)

(105) *Perithemis tenera* (Say, 1839)
(108) *Sympetrum ambiguum* (Rambur, 1842)
(109) *Sympetrum corruptum* (Hagen, 1861)
(109a) *Sympetrum costiferum* (Hagen, 1861)
(110) *Sympetrum internum* Montgomery, 1943
(111) *Sympetrum obtrusum* (Hagen, 1867)
(112) *Sympetrum rubicundulum* (Say, 1839)
(113) *Sympetrum semicinctum* (Say, 1839)
(114) *Sympetrum vicinum* (Hagen, 1861)
(123) *Tramea carolina* (Linnaeus, 1763)
(124) *Tramea lacerata* Hagen, 1861
(125) *Tramea onusta* Hagen, 1861

Excluded Species

(67) *Gomphus williamsoni* Muttkowski. This species was described by Williamson (1903) from a single male specimen collected near Bluffton. Muttkowski (1910) named it and treated it as a distinct species, but no other specimen has ever been found. Needham examined the specimen (Needham and Westfall, 1955) and concluded that it was not a valid species.

(82a) *Macromia georgina* (Selys). This species has been placed in synonymy with *Macromia illinoiensis* (Donnelly and Tennessen, 1994).

(90) *Epitheca simulans* (Muttkowski). This species has been placed in synonymy with *Epitheca cynosura* (Garrison, 1991).

(120) *Celithemis monomelaena* Williamson. This species has been placed in synonymy with *Celithemis fasciata* (Garrison, 1991).

DISCUSSION

Somatachlora hineana is included on the updated list, but the record is suspect in my opinion. A single male specimen was given to Montgomery in the early 1950s by William Kowlek, who said that this dragonfly had been collected at Gary on 22 June 1945 (Montgomery, 1953). No other record for this species exists for Indiana. Williamson (1931) originally described the species from specimens he collected in Ohio, but the species is now believed to be extirpated there (Glotzholber, 1995). Populations have recently been discovered in Illinois and Wisconsin (Vogt and Cashatt, 1994), but the species is one of the rarest in North America. *Somatachlora hineana* is the only Indiana dragonfly on the Federal List of Endangered Species (1995).

Macromia wabashensis Williamson is included on the current list, but its status as a species is questionable. Garrison (1995) stated that *M. wabashensis* is either a junior synonym of *M. taeniolata* Rambur or a hybrid between *M. taeniolata* and *M. pacifica* Hagen. Cook (1994), on the other hand, continues to

give *M. wabashensis* full species status. Both authors state that more work is needed to clarify the status of *M. wabashensis*. Discovery of the female and the larva is critical. Lacking a resolution of the matter at this time, the status quo needs to be maintained. Therefore, *M. wabashensis* has been retained on the State list of species.

One new species has been recorded and added to the State list since 1971. David Banks of The Nature Conservancy (pers. comm.) collected a single female specimen of *Stylurus scudderi* on 15 July 1995 in Lagrange County. The identity of this specimen was confirmed by Carl Cook (U.S. Fish and Wildlife Service).

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EUROPEAN SPRUCE BARK BEETLE (*IPS TYPOGRAPHUS* (L.)) INTERCEPTIONS IN INDIANA 1995[1]

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ABSTRACT: The European spruce bark beetle (*Ips typographus*), an exotic Eurasian species, is not known to occur in North America. The species is a potentially serious pest of spruce and, less frequently, other conifer species. European spruce bark beetle has been intercepted in survey traps at various ports in North America, including recent interceptions in New Jersey (1994) and Pennsylvania (1993). Surveys for spruce bark beetle have been conducted at Indiana ports since 1993 as part of a cooperative State and USDA, APHIS, PPQ Northeastern Region Bark Beetle Initiative. Negative findings were reported each year in Indiana until 17 April 1995, when one adult was intercepted in a trap within the Indiana Dunes National Lakeshore. This is the same geographic area from which early detections of the regulated pest species, pine shoot beetle (*Tomicus piniperda*), first occurred in Indiana. Following detection of the first European spruce bark beetle, an intensive trapping program was initiated. Thirteen beetles were trapped during 1995, eleven of which were taken directly at the port. No evidence of an infestation was found. All interceptions were apparently related to beetles arriving at the Port of Indiana in ships.

KEYWORDS: Exotic, Indiana, *Ips typographus*, regulatory, Scolytidae.

INTRODUCTION

Although many potential pest problems are addressed daily by Federal and State plant health regulatory officials, few instances of how the regulatory process works to mitigate an intercepted pest species have been presented in the scientific literature (see Appendix). Successful handling of new pest interceptions frequently results in activities which arouse little awareness in the general public. Success is a combination of fortuitous timing and good science, utilizing pest risk assessments and effective action plans. Action plans for the abatement and mitigation of an introduced pest are driven, in part, by the biology of the pest, its likelihood of causing extensive damage, and its ability to be intercepted and controlled through various identifiable pathways (National Plant Board, 1995). Knowledge of the regulatory process is critical to a long-term understanding of

[1] A separate presentation of this paper was made by the author at the annual meeting of the Central Plant Board (held in Des Moines, Iowa, on 4-7 February 1996) and will appear in report format in the minutes of that meeting.

regulatory actions as science and how such actions may benefit the general public as well as the regulated communities.

A discussion of a pest bark beetle, the European spruce bark beetle (*Ips typographus* (L.)), which was intercepted in Indiana, follows. This species is of considerable national interest because of its possible economic effect on coniferous forest timber resources.

BIOLOGICAL CONCERNS

Biological concerns regarding the European spruce bark beetle in North America have been well documented (e.g., anonymous, 1993; Whittle and Anderson, 1985). Christiansen and Bakke (1988) provide an overview of the biology and economic effects of this species in Eurasia, which may also apply to its possible biological activity in North America, if it should become established.

Two or three broods are produced by European spruce bark beetles in a single season. The adults overwinter in leaf litter and under bark near the sites where they emerged. They disperse in spring when temperatures rise to ca. 20° C (68° F) or approximately early April in Indiana. Dispersal flights may range from several meters to several kilometers depending on the food reserves of the individual beetle. Dispersal flight will continue until suitable host material is found or until the beetle expires. Beetles prefer weak, recently killed or felled spruce trees and slash in non-outbreak populations but will attack and kill trees when outbreaks occur (e.g., Christiansen and Bakke, 1988; Annila and Petaiso, 1978; Löyttyniemi and Uusvaara, 1977).

The European spruce bark beetle exhibits two behavioral phases: a dispersalist phase and a colonizing phase (Botterweg, 1982; Christiansen, 1991; Christiansen and Bakke, 1988; Gries, 1985). The dispersalist phase is comprised of single individuals and rarely results in the establishment of the species in the absence of diseased, stressed, or damaged spruce trees due to the inability of a single beetle to successfully colonize healthy trees (Bombosch, 1991). However, the colonizing phase is comprised of multiple individuals. During this phase, the beetles exhibit pheromone responsive attack behaviors which frequently result in establishment on diseased and damaged host materials or on healthy hosts. Large populations may become established (Anderbrant, *et al.,* 1988). With large populations, even heathy trees may be successfully colonized. When populations of this beetle are large, and host material is available, epidemics may last for extended periods of time. Exemplars of lengthy epidemics include ranges from seven to fifty years (Christiansen and Bakke, 1988). However, control of epidemic populations can be regained by good forest sanitation practices; i.e., the removal of freshly killed or felled trees, broken limbs, and so forth (Christiansen and Bakke, 1988). Beyond the damage caused by direct infestations, the European spruce bark beetle is known to vector several species of blue stain fungus (*Ophiostoma* spp.). The presence of the fungus can lead to additional adverse economic effects (e.g., loss of marketable timber and reduced recreational use (Christiansen, 1991)).

HISTORY OF BARK BEETLE STUDIES IN INDIANA

The earliest faunistic treatise including Indiana bark beetles was that of Blatchley and Leng (1916). Deyrup (1981) performed the most recent survey of the bark beetles of Indiana followed by distribution and biological updates (Deyrup and Atkinson, 1987a, b). Ninety-two species of bark beetles were recognized from Indiana as of 1987 (Deyrup and Atkinson, 1987a). Two additional records of exotic bark beetle species, *Xyleborus atratus* Eichhoff and *Xylosandrus crassiusculus* (Motchulsky), were obtained in Indiana as a result of the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine (USDA, APHIS, PPQ) Northeastern Region Bark Beetle Initiative. The results will be reported by Cavey and Passoa (in prep.). Another introduced bark beetle, pine shoot beetle (*Tomicus piniperda* (L.)) was also reported from Indiana as the subject of a Federal and State quarantine (see Sadof and Waltz, 1992; Sadof, *et al.*, 1995). Like the spruce bark beetle, this latter species was believed to have been introduced through Burns Harbor. A total of ninety-five bark beetle species are recognized as established in Indiana as of this writing. The spruce bark beetle is not known to be established in Indiana or anywhere else in North America.

Dunnage. The continued introduction of exotic bark beetles from infested wood products carried within a ship's hold (dunnage) is problematic (e.g., Sadof, *et al.*, 1995; USDA, APHIS, PPQ, 1995). However, a final rule regulating dunnage and other non-manufactured wood articles has been enacted (USDA, APHIS, PPQ, 1995), which should lead to reduced pest introductions via dunnage.

1995 Interceptions. In 1995, a single European spruce bark beetle was intercepted in a baited trap monitored by the USDA, APHIS, PPQ as part of a northeast region (USDA region) State-Federal cooperative program on introduced bark beetles. Following the initial interception, approximately 200 additional baited traps were placed within a twenty-mile radius of the Port of Indiana and monitored for additional interceptions. Twelve additional beetles were intercepted; ten beetles were trapped within the Port of Indiana perimeter, and two beetles were found on private property in separate locations within a few miles of the port.

Several attempts to scout and locate possible host sites within the twenty-mile radius of the port resulted in the discovery of a few old, recently felled Norway spruce (*Picea abies*) trees at the Dunes National Lakeshore. These trees were examined and found to be infested with *Ips grandicollis* Eichhoff, but no signs of galleries or excavations by *Ips typographus* were found. The trees were burned within days of their discovery by National Lakeshore personnel.

A total of 13 European spruce bark beetles were reported from Indiana. The capture of the majority of trapped beetles appeared to coincide with the arrival of a ship from the Ukraine. No further beetles were discovered in 1995 or in 1996 in follow-up surveys. No evidence of any established population of this species in Indiana was found.

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APPENDIX

CHRONOLOGY OF INTERAGENCY COOPERATION

Upon detection and confirmation of the first spruce bark beetle (collected on 17 April 1995), an electronic message was forwarded by USDA, APHIS, PPQ to all States providing notification of the confirmed interception in Indiana. The State Entomologist, Indiana Department of Natural Resources (IDNR), was notified prior to the release of the electronic message regarding the confirmed find and began coordination activities with the State Plant Health Director (USDA, APHIS, PPQ).

Immediately following confirmation, additional lindgren funnel traps were placed within the Burns Harbor and Dunes National Lakeshore area. Calls to other federal agencies for additional traps were coordinated by the USDA State Plant Health Director, who also placed orders for lures attractive to the spruce bark beetle to be used in the delimiting survey. Communication was maintained between USDA, APHIS, PPQ, IDNR, USDA Forest Service, and Dunes National Lakeshore personnel as the traps and other support and operations materials arrived and were placed. Data on biology, controls, and pathway information were gathered by the State Entomologist. Trapping protocols used previously by the USDA in other States with this species were obtained by the USDA State Plant Health Director.

After placing the traps in the area of the initial interception and nearby surrounding sites, additional beetles were detected. Further resources were required to expand the delimiting survey.

A response team coordinated by USDA, APHIS, PPQ (Jerry Fowler, Chair) was assembled. This team was comprised of Federal and State cooperators and functioned as the New Pest Advisory Group (NPAG). A teleconference among the members of the NPAG was held on 25 May 1995 to appraise the situation and establish a plan of action. NPAG members were asked to consider and discuss possible courses of action, including trapping protocols at different levels of intensity and coverage.

A subsequent meeting was scheduled between USDA, APHIS, PPQ (Gary Simon), USDA Forest Service (Mike Connor), IDNR (Robert Waltz), and the Indiana Dunes National Lakeshore (Randy Knutson) to finalize details of a trapping plan and to locate resources for implementation. This meeting was held on May 26 at the Indiana Dunes National Lakeshore. A report drafted by the USDA Forest Service, which provided a summary of the meeting, was filed by Mike Connor. Results of this meeting were forwarded to the NPAG and to the USDA Forest Service for further comment and final approval.

During the week of May 29, verbal notifications with written executive summaries of the pest status and interception as well as a copy of a draft news release were provided to regional Cooperative Extension Service personnel, Cliff Sadof (Purdue University), IDNR Executives, and the Office of the Indiana Commissioner of Agriculture. For all parties involved, this was not the first notification

of the interception but a notification of a possible change in program activity levels and a beginning of the public education process.

Possible host sites for this species, which were identified by aerial and ground surveillance, are extremely limited in northern Indiana, especially for the preferred host, spruce. Potential host sites included wind breaks, landscape plantings, and a few plantings in recreational areas, on State fish and wildlife properties, and on private property. For this pest, Christmas tree production areas and production nurseries were not deemed to be preferred host sites, although selected properties were monitored for purposes of confirmation.

Approval to fill two temporary positions was granted to the State Plant Health Director by USDA, APHIS, PPQ. Funds for materials and additional traps were provided by the USDA Forest Service. Materials and people were ready for deployment by June 7.

On June 10, a news article by the Associated Press appeared in the *Indianapolis Star* informing the general public of the spruce bark beetle detection and the planned trapping. The article was of particular interest to nurserymen and Christmas tree producers in Indiana, who had experienced the development of pine shoot beetle regulations and might encounter misinformation regarding the spruce bark beetle introduction and the intent of the delimiting surveys. Other news stories and at least one radio interview were conducted regarding the interception and delimiting survey activities.

Delimiting traps were placed by USDA, APHIS, PPQ during the week of 12 June 1995 and were removed by the week of September 4. A total of 184 traps were placed; 78 traps were placed within a 10-mile radius of the port, and another 106 traps were placed at possible host sites within the 25-mile radius. Twelve additional beetles were collected after the trapping commenced; 11 beetles were intercepted at the port, and one beetle was intercepted in a trap at a private residence in Chesterton.

A summary meeting was held on 11 August 1995 at the Indiana Dunes National Lakeshore, which included all the May 26 attendees as well as Dennis Haugen (USDA Forest Service) and Charlotte Gallowitch (USDA, APHIS, PPQ). A review of the present status and program activities to date was presented and discussed as were survey plans for 1996.

An on-site review of possible host material at the Indiana Dunes National Lakeshore resulted in the discovery of a significant population of *Ips grandicollis* (Eichhoff) in recently a felled Norway spruce (*Picea abies*). However, no spruce bark beetles or galleries created by spruce bark beetle were found. The felled spruce was burned by Indiana Dunes National Lakeshore personnel within three days of its discovery.

FINAL ANALYSIS

In final analysis, this author believes the regulatory system was a success. A few of the more critical factors in that success are cited below.

Prior pest survey for this species established the fact that detected beetles were new introductions and were not coming from established, incipient populations. Similarly, more generalized faunal surveys of the Indiana species of bark beetles confirmed the absence of the introduced pest in collections taken over a period of years.

Literature and data on the beetle were readily available through the USDA, APHIS, PPQ, USDA Forest Service researchers, abstracting services, and so forth, including pest risk analyses completed several years previously (e.g., Whittle and Anderson, 1985). Funding for the port and domestic bark beetle trapping program via the Cooperative Agricultural Pest Survey (CAPS) and USDA program funds was instrumental in validating pest distribution within the northeast region. However, further trapping should be attempted by all States with ports or exposure to the St. Lawrence Seaway, before they are declared free from this pest. As demonstrated in the Indiana case, negative data based on prior pest and faunistic surveys allowed a clear assessment of the interception status and reduced the need for more extensive and costly trapping protocols.

The team management concept, practiced in the USDA's New Pest Advisory Group, allowed a gathering of technical experts and policy makers to formulate appropriate response plans and to allocate resources where they were needed as quickly as possible. Resources were allocated across agencies and across Federal and State cooperative lines. Prior USDA/State experience in working through interceptions of this beetle in Pennsylvania (1993) and New Jersey (1994) were beneficial in establishing a proven track record of interception and detection/delimit trapping for this species.

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UNUSUAL CARBONATE BUILDUPS IN THE UPPER MANSFIELD AND BRAZIL FORMATIONS, VANDERBURGH COUNTY, INDIANA

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ABSTRACT: Unusually thick limestone is present in the Upper Mansfield and Brazil Formations within and adjacent to the Vaughn Consolidated Field (T7S, R11W), Vanderburgh County, Indiana. Continuous carbonate buildups exceeding 40 feet in the Mansfield and 60 feet in the Brazil extend from the SW 1/4 Sec. 15 into the NE 1/4 Sec. 21. Examination of well samples shows that echinodermal-brachipodal-bryozoan grainstones and packstones dominate continuous limestone intervals more than 30 feet thick. Maps based on 125 wells show the distribution of net thickness of both limestone and sandstone and document complex facies relationships and changes of loci of carbonate accumulation through time.

KEYWORDS: Brazil Formation, carbonate buildups, Mansfield Formation, Pennsylvanian.

INTRODUCTION

Unusually thick intervals of limestone occur in Lower Pennsylvanian rocks in and adjacent to the Vaughn Consolidated Field in southwestern Vanderburgh County, Indiana. Petroleum production from Lower Pennsylvanian and Mississippian reservoirs began in 1941, and some production history is given in Keller (1995). The study area (Figure 1) of approximately eight square miles is located in all or parts of 12 sections centered in T7S, R11W. The Indiana Geological Survey maintains electric logs for 125 wells in the study area and samples from 63 of these wells drilled when the Survey was requesting samples for every well drilled. A microscopic study was made on sample sets from those wells in which limestone was abundant. For comparison, a less thorough examination was made of sample sets from wells containing thin or no limestone intervals. In the samples examined, major emphasis was placed on determining identifiable biotic constituents from the fragmented limestones.

STRATIGRAPHY

A recent study (Droste and Furer, 1995) traced the outcrop stratigraphy of the Staunton, Brazil, and Mansfield Formations throughout the subsurface in southwestern Indiana. These correlations were utilized to establish stratigraphic relationships in the study area. Much of the formation stratigraphy along the

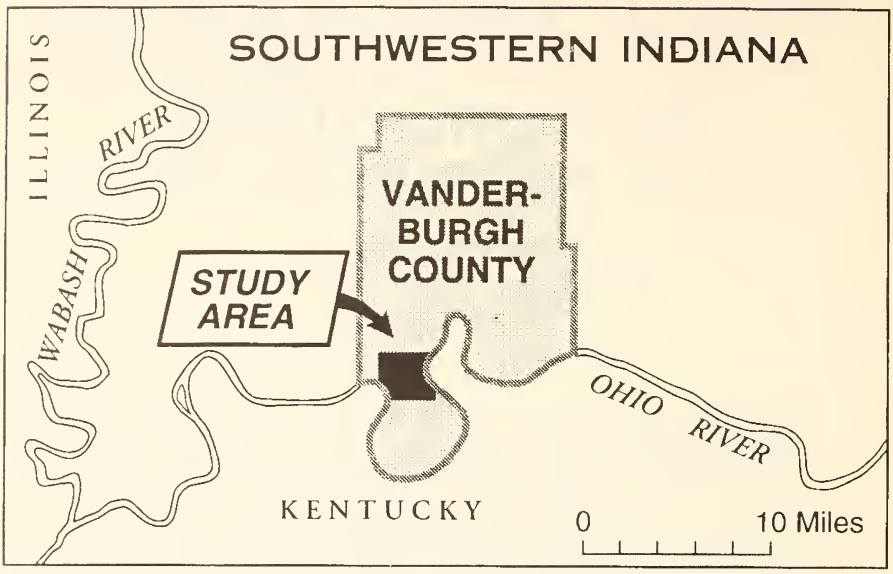

Figure 1. Map showing the location of the study area.

outcrop is based on the position of coals and a few limestone members (Figure 2). In the subsurface of the study area, no coals were identified in the samples studied, and the correlated positions of the coals are generally occupied by intervals of limestone and/or marine shale. Electric logs from three wells (Figure 3) in Sec. 15, T7S, R11W illustrate the lateral variation in lithologies over lateral distances of no more than 0.5 miles between wells.

Brazil Formation. The top of the Brazil Formation is placed at the base of either the Perth Limestone or the sandstone occupying the stratigraphic position of the Perth. Because the Perth is not recognized in the study area, the base of the sandstone in the Perth position marks the top of the Brazil Formation (Figure 3). Along its outcrop, the base of the Brazil is placed at the base of the Lower Block Coal (Figure 2). However, the Lower Block Coal is not present in the study area, and limestone, shale, or sandstone occupies its stratigraphic position. In this study, the base of the Brazil Formation is placed at the correlated stratigraphic position of the Lower Block Coal (Figure 3). The Brazil ranges in thickness in the study area from 90 to 110 feet.

In many places in the study area, the position of the Buffaloville Coal is occupied by limestone (e.g., its occurrence in the #2 Kamp and Happe Well (Figure 3)). In the #2 Kamp and Rollette well (Figure 3), the interval correlated with the Upper and Lower Block Coals is continuous limestone, but in the Bell and Sirkle well, this interval is all sandstone. The net thickness of limestone and sandstone in the Brazil (Figure 4) is discussed below.

Mansfield Formation. Because the Mansfield Formation is more than 800 feet thick in the subsurface of Indiana, the formation was divided informally

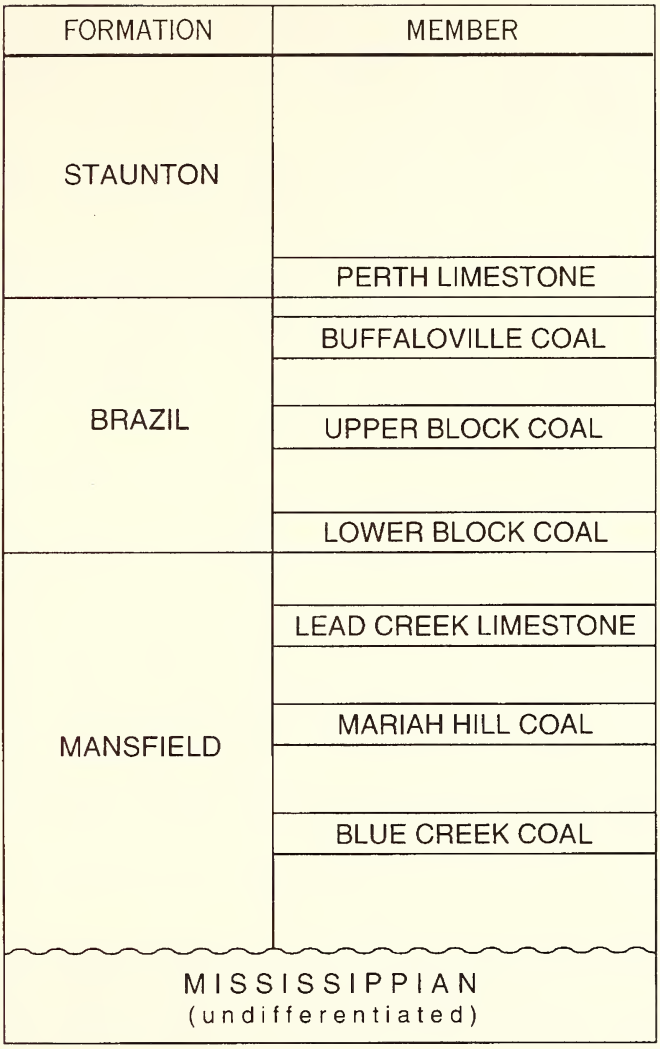

Figure 2. Chart of stratigraphic nomenclature used in this report.

into upper, middle, and lower divisions (Droste and Furer, 1995). The interval of thick limestone in southern Vanderburgh County occurs in the upper division. The top of the Mansfield is placed at the stratigraphic position of the base of the Lower Block Coal (Figure 2), and the base of the upper Mansfield is placed at the stratigraphic position of the top of the Blue Creek Coal (Figure 2). The Mariah Hill Coal (Figure 2), exposed along the upper Mansfield outcrop, is replaced by limestone in many places in the subsurface of southwestern Indiana, and its position marks the lowest position of limestone in the upper Mansfield of the study area. The upper Mansfield ranges in thickness from 110 to 130 feet in this area. The three well records in Section 15 (Figure 3) document the

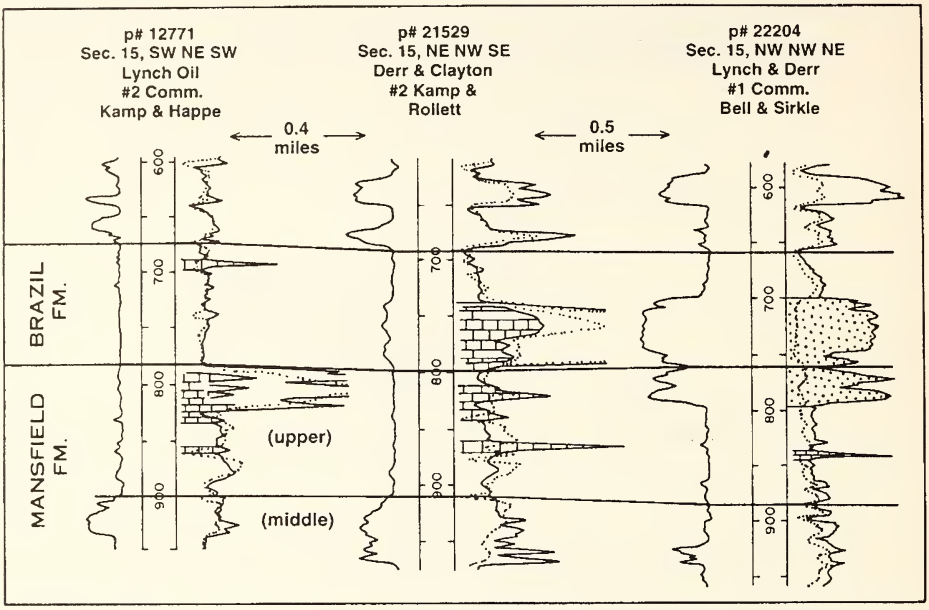

Figure 3. Electric logs from three wells showing marked lithologic differences in the Brazil and Mansfield Formations.

facies changes that occur from well to well within no more than 0.5 miles. The net thickness (Figure 5) of limestone and sandstone in the upper Mansfield are discussed below.

DISCUSSION

The same kinds of sandstone, limestone, and shale occur in both the Brazil and the upper Mansfield Formations. Very fine- to fine-grained, moderately to well-sorted quartz grains compose the sandstone. The shales are typically medium to dark gray in color and are sparingly to moderately silty. The limestones range from wackestones to grainstones. Debris of echinoderms, brachiopods (including productid spines), and bryozoans has been observed in various samples of the carbonate lithologies. This typical late Paleozoic faunal association is interpreted as occurring on shallow marine shelves (Lane, 1992).

Available samples (cuttings) and sample intervals (typically 10 feet) limit detailed interpretations. However, limestones present in single intervals less than 10 feet thick are mostly wackestones. In thicker limestone intervals, wackestones appear to be most abundant in the lower part of the interval and packstones and grainstones increase upwards. In the thickest limestone intervals, grainstones are dominant in the upper limestone beds.

The area of greatest net limestone thickness in the upper Mansfield (Figure 5A) extends from the southern half of Section 15 southwestward into Sections 21 and 20, and net thicknesses greater than 20 feet generally fall within a zone

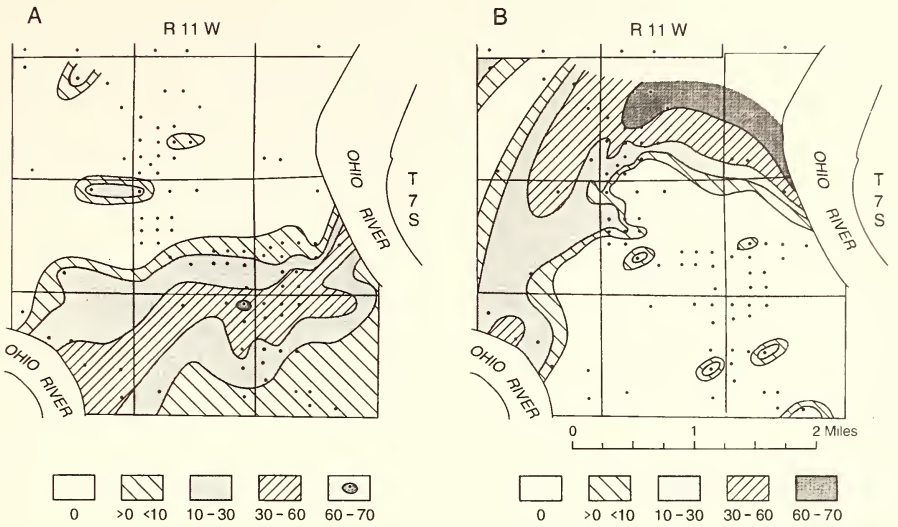

Figure 4. Maps showing net thickness in feet of limestone (A) and sandstone (B) in the Brazil Formation.

about 0.5 miles wide. The area of greatest net limestone thickness in the Brazil (Figure 4A) overlies that of the Mansfield. However, the width of the zone containing more than 20 feet of limestone increases by approximately 50% in the Brazil.

Zones of thicker sandstones in the Mansfield lie both to the north and south of the zone of thicker limestones (compare Figures 5A and 5B), and no sandstone is present in the upper Mansfield in much of the zone of thicker limestone.

The thicker sandstone in the Brazil lies in a zone generally north of the zone of thicker limestone, and a shale facies generally lies between the limestone and sandstone thickenings. In the northwest quarter of Section 20, sandstone is present in the lower part of the Brazil and is in facies relationship with limestone in the southeast quarter.

The available information does not suggest that the carbonates represent wave-resistant reefs. The typical Upper Paleozoic marine faunal association is interpreted as living on or within the areas of carbonate deposition, including calcareous sands or bars among which were quieter waters that yielded carbonate muds.

The authors are unaware of any literature describing intervals of limestone ten or more feet thick in the Mansfield or Brazil Formations in the subsurface or surface in Indiana. Why are these thick limestones in southernmost Vanderburgh County? We suggest that crinoids, bryozoans, and brachiopods colonized local sea floor highs that resulted from slight variations in regional rates of subsidence. These sea floor highs were probably above storm wave base so

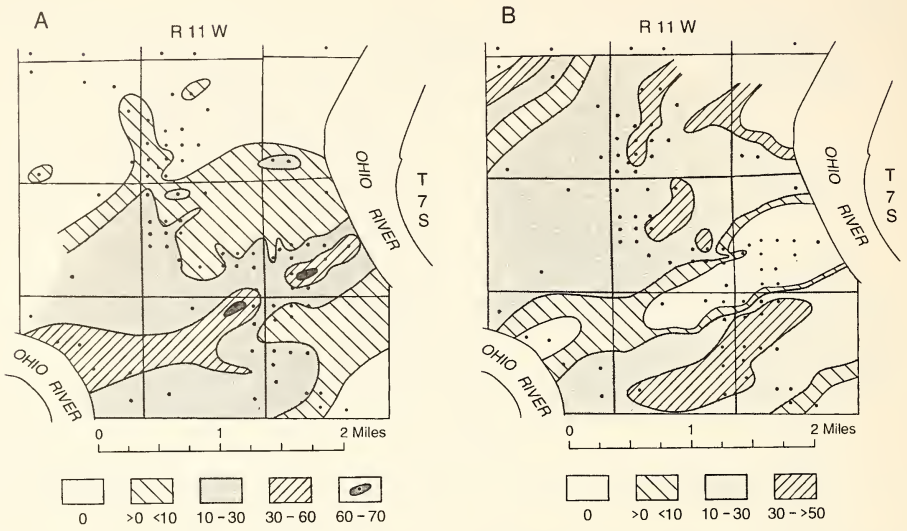

Figure 5. Maps showing net thickness in feet of limestone (A) and sandstone (B) in the upper part of the Mansfield Formation.

that terrigenous sand and mud was winnowed from or bypassed the highs, and crinoid thickets developed. As the fauna flourished, it continually contributed carbonate debris to the buildup. If the rate of accumulation exceeded the rate of subsidence, the thicket remained above storm wave base. Limestone deposition ceased because subsidence exceeded accumulation or deposition of terrigenous sediments exceeded deposition of carbonate debris possibly because of shifting currents and/or shifting sources of terrigenous sediments.

Several well logs from western Kentucky were studied that contained ten to thirty feet of limestone in the Brazil equivalents. We will continue to examine well logs in southern Indiana and western Kentucky to discover other locations of thick limestones in Lower Pennsylvanian rocks.

CONCLUSION

In the study area, shallow water marine deposition occurred during the interval from the Blue Creek Coal through the Buffaloville Coal. In some areas, the absence of the smothering effects of terrigenous sands and muds permitted inferred crinoidal thickets to dominant sedimentary processes and produce thick limestones. However, the location of crinoidal accumulations shifted somewhat through time.

ACKNOWLEDGMENTS

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BASIS FUNCTIONS FOR LOCALIZED QUANTUM POTENTIALS

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ABSTRACT: A set of orthogonal functions was constructed for use as a basis set in quantum mechanical energy calculations. Specifically, the functions have the correct asymptotic behavior appropriate for all one-dimensional localized potentials. The results of these calculations are reported for several potential wells and compared with calculations using Hermite Functions.

KEYWORDS: Computational physics, orthogonal polynomials, quantum mechanics.

INTRODUCTION

In classical physics, a particle confined to an attractive potential will oscillate, and the details of the motion, such as frequency and amplitude, are determined by the particle's energy. This energy can take any value from zero (no motion) up to the binding energy of the potential. According to quantum mechanics, however, the energy of oscillation is constrained to take on a value from a discrete set of allowed energies or eigenvalues. The calculation of the energy eigenvalues for a particular potential is a central problem of quantum mechanics, and many methods have been developed to solve it.

Fundamentally, all methods must find the eigenvalues of the time-independent Schrödinger Equation. In one dimension, this takes the form

$$-\frac{\hbar^2}{2m}\frac{d^2\psi}{dx^2} + V(x)\psi = E\psi \quad .$$

Here, m is the particle's mass, V(x) is the potential, ψ is the particle's wavefunction, and $\hbar$ is Planck's Constant divided by 2π. When appropriate boundary conditions are applied to ψ, the particle's energy, E, is found to have a discrete spectrum.

A powerful method for solving the Schrödinger Equation is the Variational Method (Schiff, 1968). This method takes advantage of the fact that the wavefunction is an element of a Hilbert Space. Specifically, one can choose a complete set of functions as a basis and express the wavefunction as a linear combination of these basis functions. The choice of basis is essentially arbitrary, but each basis function must satisfy the boundary conditions of the problem. As a practical matter, the basis is chosen to be orthonormal, for then the calculations are

greatly simplified. By orthonormal, we mean: let the nth basis function be $\phi_n(x)$, and its complex conjugate be $\phi_n^*(x)$. Then, for every pair of m and n

$$\int_{-\infty}^{\infty} \phi_m^*(x)\phi_n(x)dx = \delta_{m,n} \quad .$$

Here, $\delta_{m,n}$ is the Kronecker Delta, which equals one if m = n and is zero otherwise.

Once the basis is chosen, the calculations are almost rote. A Hamiltonian matrix, H, is constructed, the elements of which are

$$H_{m,n} = \int_{-\infty}^{\infty} \phi_m^* \left(-\frac{\hbar^2}{2m}\frac{d^2}{dx^2} + V \right) \phi_n dx \quad .$$

(Normally, for time-independent problems, ϕ is chosen to be a real function and ϕ^* becomes ϕ.) The eigenvalues of the matrix are the allowed energies of the potential, and the eigenvectors give the wavefunctions as a linear combination of the basis functions.

The size of the basis set, and hence of the H matrix, is chosen by the investigator with the understanding that only an infinite basis can be expected to produce exact eigenvalues. A finite basis set produces approximate energies, and normally, enlarging the set improves the accuracy. The rate of convergence, however, is sensitive to the choice of basis.

CHOICE OF BASIS

Since little is required of the basis functions other than the necessity of satisfying the boundary conditions, it seems reasonable to look at these conditions when selecting the basis. In this work, we are interested in all one dimensional, localized potential wells. By localized, we mean that $V(x) \rightarrow 0$ as $x \rightarrow \pm\infty$. For such potentials, the wavefunction tends to zero as $x \rightarrow \pm\infty$. However, we can be more specific. For $|x|$ large, $V \rightarrow 0$ and the energy of the system is all kinetic. Therefore, $p^2/2m \approx E$ and $p \approx \sqrt{2mE}$. Expressing this in the language of quantum operators, we have

$$-i\hbar\frac{d\psi}{dx} \approx \sqrt{2mE}\psi = i\sqrt{2m|E|}\psi$$

($E < 0$ for bound states). This equation has the solution

$$\psi = ce^{\pm kx}, \quad k = \sqrt{2m|E|}/\hbar,$$

with c an arbitrary constant. The boundary conditions require choosing the sign so that $\psi \rightarrow 0$ as $|x| \rightarrow \infty$. Therefore, $\psi \sim ce^{+kx}$ for $x < 0$ and $\psi \sim ce^{-kx}$ for $x > 0$.

A common choice of basis is $H_n(x)\, e^{-x^2/2}$, where H_n is a (normalized) Hermite Polynomial. The Hermite Polynomials satisfy the Schrödinger Equation for the case $V(x) = x^2/2$, and, therefore, are automatically orthogonal (with respect to the weight function $e^{-x^2/2}$) and form a complete set (Abramowitz and Stegun, 1964; Erdélyi, 1953; Szegö, 1975). However, since $V(x) = x^2/2$ is not localized, the Hermite Functions vanish more rapidly than e^{-x}, going to zero as e^{-x^2} as x goes to infinity. In light of the previous discussion, then, it seems reasonable to search for a set of functions that share the above properties but vanish as $e^{\pm x}$. One such function is sech(x), since

$$\mathrm{Sech}(x) = \frac{2}{e^{x} + e^{-x}} \quad .$$

Therefore, it is necessary to construct polynomials $V_n(x)$, orthogonal with respect to $\mathrm{sech}^2(x)$ for then our basis functions could be chosen as $V_n(x)\,\mathrm{sech}(x)$. The orthonormality condition becomes

$$\int_{-\infty}^{\infty} V_m(x) V_n(x) \mathrm{sech}^2(x) dx = \delta_{m,n}$$

Pickett (in press) has constructed these polynomials. The first few are

$V_0(x) = 1$
$V_1(x) = x$
$V_2(x) = x^2 - 1/12$
$V_3(x) = x^3 - (7/20)x$
$V_4(x) = x^4 - (13/14)x^2 + 27/560$

(Actually, these polynomials have been constructed to be orthogonal with respect to $\mathrm{sech}^2(\pi x)$ rather than $\mathrm{sech}^2(x)$. This constitutes a minor detail and was done to avoid cumbersome powers of π in the coefficients.) As written, these functions are not normalized. Each must be multiplied by

$$h_n = \sqrt{\frac{(2/\pi)(n!)^4}{4^n(2n+1)\left[(2n-1)!!\right]^2}}$$

All orthogonal polynomials satisfy a three term recurrence relation (Abramowitz and Stegun, 1964; Erdélyi, 1953; Szegö, 1975). The polynomials $V_n(x)$ satisfy

$$V_{n+1}(x) = xV_n(x) - C_nV_{n-1}(x), \quad C_n = \frac{n^4}{4(2n-1)(2n+1)}$$

The recurrence provides a relatively simple method for calculating the basis functions.

CALCULATIONS

We tested the polynomials by using them to calculate energies for three potentials: the finite square well, e^{-x^2}, and $sech^2(x)$. We began with sixteen functions in the basis, then enlarged it to twenty, and then to twenty-six. Each calculation was timed and compared to calculations using Hermite Functions as well as to the actual energy values. All of the basis set calculations were performed with Mathematica® on an Intel® 486 33 MHZ processor.

For purposes of numerical solution, the Schrödinger Equation must be cast into dimensionless form. Since our potentials are chosen rather than determined by data, this is easily done by adopting machine units for the various physical dimensions of the problem. In our calculations, we have set m = 1 mass unit, $\hbar = 1$ action unit, and x can be taken as a dimensionless variable measuring length units.

$V(x) = V_0 sech^2(x)$. This potential was chosen because it is localized and the energies are known exactly (Landau and Lifshitz, 1977). The well depth, V_0, was chosen as follows. For this potential, the number of bound states is given as the largest integer not exceeding s, where

$$s = \frac{1}{2}\left(1 + \sqrt{1 - 8V_0}\right)$$

We wanted all of our trial potentials to have a depth that was about midway between those that would bind six and seven states. Therefore, we chose $V_0 = -143/8$ ($s = 6\frac{1}{2}$).

In the calculations, it is possible to generalize the basis functions by writing them as $V_n(bx/\pi)sech(bx)$ with b an adjustable parameter. A similar conversion is possible for the Hermite Functions. We chose b by finding the value that minimized the maximum error in the 16 x 16 cases. That is, in each calculation, six energies are computed, and b is chosen to minimize the largest of the six errors. In general, the optimum value of b for the 16 x 16 case will not optimize the 20 x 20 case, or any other basis set size. However, once the parameter had been chosen in this way, its value was considered permanent, even when the basis was enlarged. This reflects the fact that, in practice, one doesn't know the energies in advance and has no way to compute a new parameter as the basis is

Table 1. A comparison of the calculated energies of the potential well $V(x) = (-143/8)\text{sech}^2(x)$ using Hermite Functions and Sech Functions.

	True Energies	Basis Set Size 16 x 16	20 x 20	26 x 26
Hermite Functions				
E_0	-15.125000	-15.122276	-15.124390	-15.124926
E_1	-10.125000	-10.114147	-10.122343	-10.124646
E_2	-6.125000	-6.085141	-6.114609	-6.123532
E_3	-3.125000	-3.081641	-3.112872	-3.123165
E_4	-1.125000	-1.067728	-1.108258	-1.122517
E_5	-0.125000	-0.057308	-0.096037	-0.116561
Calculational Time		220 sec	550 sec	1754 sec
Sech Functions				
E_0	-15.125000	-15.124807	-15.124951	-15.124991
E_1	-10.125000	-10.123977	-10.124714	-10.124942
E_2	-6.125000	-6.120332	-6.123705	-6.124741
E_3	-3.125000	-3.119102	-3.123217	-3.124610
E_4	-1.125000	-1.116973	-1.122574	-1.124475
E_5	-0.125000	-0.120390	-0.123903	-0.124684
Calculational Time		356 sec	1091 sec	4948 sec

Table 2. A comparison of the relative errors (%) of the calculated energies of the potential $V(x) = (-143/8)\text{sech}^2(x)$ using Hermite Functions and Sech Functions.

	Basis Set Size 16 x 16	20 x 20	26 x 26
Hermite Functions			
E_0	0.018010	0.004033	0.000492
E_1	0.107188	0.026241	0.003498
E_2	0.650764	0.169649	0.023960
E_3	1.387501	0.388096	0.058724
E_4	5.090839	1.488143	0.220687
E_5	54.153337	23.170524	6.750982
Sech Functions			
E_0	0.001273	0.000322	0.000058
E_1	0.010108	0.002825	0.000568
E_2	0.076219	0.021137	0.004227
E_3	0.188726	0.057062	0.012493
E_4	0.713498	0.215644	0.046691
E_5	3.688075	0.877895	0.252670

enlarged. The optimizing parameter for the Hermite Functions in this case has the value b = 1.197566, while that for the sech polynomials is b = 3.9291591.

The results of the calculations for this potential are shown in Tables 1 and 2 along with the correct energies and the results using the Hermite Functions. A proper comparison must also include the amount of time spent computing, and those data are also listed in the tables.

The Finite Square Well ($V(x) = 0$ for $x > 1$ and $x < -1$; for $-1 < x < 1$, $V_0 = -121\pi^2/32$). The well depth was chosen as the mean of the values that would just accommodate six and seven states. The actual energies are transcendental but can easily be calculated numerically (French and Taylor, 1978; Schiff, 1968). For this potential, the optimizing parameters take on the values b = 3.442024 for the Hermite Functions and b = 12.024734 for the sech polynomials. The results are shown in Tables 3 and 4.

$V(x) = V_0 e^{-x^2}$. Using the same criterion for depth as for the square well, we arrive at $V_0 = -27.44171$. To obtain the actual energy eigenvalues, we used a numerical method known as the Numerov Technique (French and Taylor, 1978; Griffin and McGhie, 1973). The idea is to numerically integrate the Schrödinger Equation from x = 0 out to $x \rightarrow \infty$, starting with $\psi(0) = 0$ and $\psi'(0) = 1$ for odd states and $\psi(0) = 1$ and $\psi'(0) = 0$ for even states. Energy values in the equation are chosen by trial and error; the quality of the choice is judged by how close ψ fits the boundary condition. For these potentials that condition is $\psi \rightarrow 0$ as $x \rightarrow \infty$. A poor choice of E results in ψ diverging quickly, while better choices of E keep ψ near zero over a larger range of values. Again, parameter values were chosen to minimize the maximum error in the 16 x 16 case; the values are b = 1.645977 for the Hermite Functions and b = 5.247306 for the sech polynomials. The results for this potential are shown in Tables 5 and 6. The true energy values given in the tables are accurate to the number of digits shown.

CONCLUSIONS

The results given in Tables 1-6 show some consistent patterns. First, except for the square well potential, the calculations using the sech polynomials give better energies than those using Hermite Functions. This is true for the small basis sets and remains so as the sets are enlarged, although the low energy states of the e^{-x^2} potential calculated with Hermite Functions have "caught up" in the 26 x 26 case.

The square well is the exception. We do not know what, if anything, makes this case different. With only three potentials investigated, a sweeping generalization should not be made, but should it prove true that the sech polynomials give better accuracy for the general case, the square well results are anomalous. It may be that the discontinuity in the potential's derivative is responsible; however, it is not clear why that should affect the Sech Functions so much more than the Hermite Functions. Clearly, more work is warranted here.

A second observation is that the calculations are much faster using Hermite Functions. All of the computation times, for both basis sets, show a con-

Table 3. A comparison of the calculated energies of the square well potential using Hermite Functions and Sech Functions.

	True Energies	Basis Set Size 16 x 16	20 x 20	26 x 26
Hermite Functions				
E_0	-36.329354	-36.326241	-36.327061	-36.328040
E_1	-33.370612	-33.356871	-33.361853	-33.365399
E_2	-28.481947	-28.453676	-28.460959	-28.470079
E_3	-21.746346	-21.692373	-21.709459	-21.725061
E_4	-13.346977	-13.268379	-13.286394	-13.314615
E_5	-3.853913	-3.733395	-3.737808	-3.801060
Calculational Time		199 sec	517 sec	1708 sec
Sech Functions				
E_0	-36.329354	-36.318742	-36.320752	-36.324656
E_1	-33.370612	-33.320784	-33.342425	-33.354259
E_2	-28.481947	-28.373490	-28.398686	-28.435904
E_3	-21.746346	-21.535710	-21.611499	-21.677984
E_4	-13.346977	-12.927119	-13.108181	-13.199459
E_5	-3.853913	-3.485023	-3.514844	-3.709793
Calculational Time		347 sec	1042 sec	4960 sec

Table 4. A comparison of the relative errors (%) of the calculated energies of the square well potential using Hermite Functions and Sech Functions.

	Basis Set Size 16 x 16	20 x 20	26 x 26
Hermite Functions			
E_0	0.008570	0.006313	0.003617
E_1	0.041176	0.026247	0.015622
E_2	0.099258	0.073688	0.041669
E_3	0.248192	0.169622	0.097878
E_4	0.588883	0.453909	0.242463
E_5	3.127162	3.012638	1.371418
Sech Functions			
E_0	0.029212	0.023679	0.012931
E_1	0.149318	0.084466	0.049002
E_2	0.380791	0.292327	0.161655
E_3	0.968603	0.620089	0.314360
E_4	3.145717	1.789137	1.105252
E_5	9.571833	8.798044	3.739581

Table 5. A comparison of the calculated energies of the potential well $V(x) = V_0\exp(-x^2)$ using Hermite Functions and Sech Functions.

	True Energies	Basic Set Size 16 x 16	20 x 20	26 x 26
Hermite Functions				
E_0	-23.92594	-23.925830	-23.925927	-23.925938
E_1	-17.29571	-17.295096	-17.295643	-17.295705
E_2	-11.50453	-11.499700	-11.503953	-11.504522
E_3	-6.642870	-6.635298	-6.641860	-6.642747
E_4	-2.856653	-2.834841	-2.853567	-2.856632
E_5	-0.442474	-0.393145	-0.425211	-0.437564
Calculational Time		227 sec	558 sec	1763 sec
Sech Functions				
E_0	-23.92594	-23.925920	-23.925930	-23.925936
E_1	-17.29571	-17.295640	-17.295666	-17.295696
E_2	-11.50453	-11.504378	-11.504399	-11.504461
E_3	-6.642870	-6.642563	-6.642688	-6.642748
E_4	-2.856653	-2.854934	-2.856453	-2.856485
E_5	-0.442474	-0.441446	-0.442270	-0.442378
Calculational Time		367 sec	1078 sec	5004 sec

Table 6. A comparison of the relative errors (%) of calculated energies of the potential $V(x) = V_0\exp(-x^2)$ using Hermite Functions and Sech Functions.

	Basis Set Size 16 x 16	20 x 20	26 x 26
Hermite Functions			
E_0	0.000461	0.000051	0.000007
E_1	0.003549	0.000388	0.000027
E_2	0.041981	0.005019	0.000071
E_3	0.113993	0.015200	0.001838
E_4	0.763535	0.108046	0.000751
E_5	11.148594	3.901441	1.109789
Sech Functions			
E_0	0.000085	0.000043	0.000016
E_1	0.000404	0.000253	0.000080
E_2	0.001319	0.001142	0.000602
E_3	0.004618	0.002735	0.001843
E_4	0.060183	0.007016	0.005864
E_5	0.232454	0.046211	0.021732

sistent trend, independent of potential. Therefore, we conclude that the time-limiting step involves the evaluation and integration of the basis functions. It is not known to the authors what method Mathematica uses to evaluate Hermite Polynomials, but the numerical analysis references such as Abramowitz and Stegun (1964) give very efficient methods for well known functions such as these. The Sech Polynomials have not been so thoroughly studied; in our investigations, we could find no faster method than the recurrence relation. Should a faster method become available in the future, Sech Polynomials may provide the best basis functions for calculating bound state energies of localized potentials.

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STUDENT EVALUATION OF AN UNDERGRADUATE EARTH SCIENCE CLASS AS A FUNCTION OF TOPIC DIFFICULTY AND TOPIC INTEREST

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ABSTRACT: A survey of over 250 undergraduate students enrolled in an earth science class for non-majors revealed a wide range of attitudes with respect to 15 key topics presented during lecture and lab. The students provided attitudinal data on their interest in the various topics as well as on how difficult each topic was to understand. Whether or not a topic was perceived as interesting was not dependent on whether or not it was easy to understand. Class material which called for spatial visualization was considered quite difficult by the students.

KEYWORDS: Attitude, earth science, science education, undergraduate.

INTRODUCTION

Undergraduates often enroll in science courses simply to fulfill degree requirements. Commonly, these introductory courses are designed with the non-major in mind, and they provide non-majors with both lecture and laboratory experiences. In an effort to better understand the views of undergraduate non-majors on the topics covered in one earth science class, an attitudinal survey was administered to over 250 students. The survey asked the students to rate the lectures and labs as a function of topic interest and difficulty.

The attitudes of students should not be the sole factor shaping content in an earth science course; however, such data can be used to raise both the level of student learning and the quality of teaching. Because these courses are only a minor component in the student's course work, such classes must engender an interest in earth science (or science in general) which will last a lifetime.

The student perceptions described in this paper should be useful to all earth science teachers. Even if the geology courses at your institution differ greatly in content from the courses discussed here, the techniques outlined in this paper should serve as a useful guide for the construction of related surveys. The data presented here also represent a baseline against which further studies can be compared.

RATIONALE AND PREVIOUS WORK

Two factors that affect a course's success are the students' perceptions of topic difficulty and topic interest. If a topic is viewed as difficult to understand, then the instructor should bear this perception in mind when he/she teaches. Dif-

ficult topics could potentially frustrate the students and turn them off to the field. The topics viewed as less difficult may point to presentations using more successful teaching techniques that could be expanded to other parts of the course. Just as students perceptions of topic difficulty are useful in planning a course, knowledge of their interests can also be helpful. Using topics whose interest levels are highly rated, an instructor may be able to identify teaching techniques and subject material that would make other parts of the course more interesting to the students. Finally, a comparison of class topics ordered by both difficulty and interest can aid earth science instructors. Topics of low interest and great difficulty may need to be reorganized so that greater interest can be generated. When difficult topics are rated high in interest, a key teaching technique used for those topics might increase the appeal of other topics.

A number of researchers have developed and/or utilized attitudinal instruments to obtain information helpful to science teachers. Instruments have been designed and administered to collect attitudinal data from elementary school students (Davis, Lang, Taylor, Knight, and Sims, 1992), secondary school students (Towse, 1983; Renner, Abraham, and Birnie, 1985), teachers in training (Lucas and Dooley, 1982; Koballa, 1984), and active teachers (Lombard, 1982; Finley, Stewart, and Yarroch, 1982).

Some research has also been carried out on student attitudes and earth science topics. Fortner and Mayer (1991) conducted a longitudinal study of the attitudes and understanding of fifth and ninth graders on oceans and the Great Lakes, using an attitudinal instrument based on semantic differential items. Crawley and Coe (1990) studied the attitudes of middle school earth science students toward enrolling in high school science classes.

Studies involving college students in earth science courses are also found in the literature. Kern and Carpenter (1984) reported on the attitudes, values, and interests of undergraduates to 30 topics in an earth science course in which roughly half of the surveyed students were enrolled in a traditional earth science laboratory, while the others were enrolled in a field-oriented lab. Carpenter (1982) discussed attitudinal changes in undergraduates towards a physical geology and environmental earth science class over time. Buchwald and Bybee (1990) discussed the role of geologists in the reform of science education, emphasizing the need to develop positive attitudes about knowledge and inquiry in children.

Table 1 lists the topics which were used to assess attitudes among the undergraduates participating in this study. Although several studies have focused on how to teach a number of these topics, none appear to have involved the collection of attitudinal data. For example, Eves and Davis (1987) discussed teaching about igneous rock in the lab, while Birdd (1990) described activities that could be used to present information on the rock cycle as well as on the development of metamorphic rock. Activities on sedimentary rock formation were outlined by Perdue (1991), while mineral identification has been discussed by numerous authors (e.g., Pasteris, 1983). Happs (1982) compared the views of children and scientists in regard to glaciation; wind erosion activities were

described by McLure (1991); shoreline depositional models have been discussed by Miall (1982); and Bart (1991) has outlined topographic map activities. Although college texts discuss relative age and cross-cutting, few studies have discussed how to improve the teaching of these topics in the classroom (Newman, 1983; Oringer, 1985). Many activities have been published on mineral resources (Sherman and Stone, 1992).

METHODOLOGY

Instrument Development. The survey required the students to rate 15 key topics (Table 1) by difficulty and interest using a four-step scale: very difficult, difficult, easy, and very easy. The selected topics covered almost all of the major weekly lecture and laboratory topics. Before the final survey was completed, a draft was returned to the course instructor for reaction and feedback. Following the instructor's review, the survey was evaluated by seven student judges, who had completed an earth science course and were familiar with the rating scales. The student judges were asked to evaluate the clarity of written directions, the ease with which the rating categories could be used, and the wording of each item. Most of the changes suggested by the judges were made in the survey format. An example of one change was in the visual format of the survey. The judges suggested that a different font be used for the rating category descriptors. The modified version of the instrument was then re-evaluated by the judges. The survey was revised and then piloted using ten students who had taken this course. Written comments were solicited from these ten students.

Data Collection. The final version of the survey was administered to students attending a large Midwestern university during the twelfth week of classes (three weeks prior to the end of the semester). Students in 24 laboratory sections were asked to respond to the survey. None of the sections contained more than 20 students. Over 250 students attended lab sessions during the week the surveys were distributed. Of these students, 95% completed the survey.

The text, lab manual, and instructor are important factors which affect students' attitudes toward class topics. To see how applicable the responses were to earth science courses in general, the survey was also administered to students attending a large state university in the southern United States. In general, the same type of student (non-major) enrolled in both courses, and both classes were organized in a similar manner. Not all of the topics covered at the Midwestern university were presented at the Southern university, but at both institutions, similar class formats and texts (Lutgens and Tarbuck, 1989; Tarbuck and Lutgens, 1993) were utilized. Fifty-six students at the Southern university completed the survey. Data from the Midwestern university are presented first followed by the data from the Southern university.

Data Evaluation. The stochastic Rasch model (Rasch, 1960) was used to evaluate these data. This method was used because ordinal attitudinal scales first must be converted to interval scales, especially if one wishes to use parametric tests to analyze the data. The necessity of conversion can best be understood

Table 1. The list of topics surveyed at a Midwestern university. Topics 11-15 were labs. One survey asked students to indicate their level of interest in each of the topics by choosing from four possible responses: 1) very disinteresting; 2) disinteresting; 3) interesting; or 4) very interesting. A second survey asked students to indicate how difficult each topic was to understand by selecting from four possible responses: 1) very difficult; 2) difficult; 3) easy; or 4) very easy. The topics presented to the students at a second institution are listed in Table 4.

1	The difference between rocks and minerals
2	The rock cycle
3	Using cross-cutting relationships to determine the relative age of rocks
4	The way sedimentary rocks are formed
5	The way igneous rocks are formed
6	The way metamorphic rocks are formed
7	Mineral resources in the world
8	The landforms caused by glaciers
9	The role wind plays in erosion
10	The way shorelines are created
11	How to identify minerals (lab 1)
12	How to identify igneous rocks (lab 2)
13	How to identify sedimentary rocks (lab 3)
14	How to identify metamorphic rocks (lab 4)
15	How to read a topographic map (lab 5)

by noting that a step in attitude from very easy to easy does not necessarily represent the same quantifiable change in attitude as a step from easy to difficult (Thurstone, 1925, 1926, 1928; Wright and Masters, 1982). This problem is often overlooked because false linearity of scales is often suggested by the computer coding of attitudinal data. The Rasch method was also selected because: 1) evaluation is possible even when the respondents do not answer every item; 2) measurement errors of survey items and respondents are reported; and 3) idiosyncratic responses by the students can be easily detected (Wright and Masters, 1982). Many researchers have utilized this method to solve a variety of problems connected with the calibration of test items (Kelley, 1979; Wongbundhit, 1985). Rasch measures have also been applied in science education (Preece, 1979; Monk, 1984; Meyer, 1989). The Bigsteps computer program (Wright and Linacre, 1991) was utilized to calibrate measures of both respondents and items.

When categories such as very easy, easy, difficult, and very difficult are coded, many evaluators assign weights to each response. A very easy might be named a 1, while an easy is considered a 2. A rating of difficult is assigned a 3, and a very difficult is called a 4. Naming categories with numbers is fine. However, one can not immediately use these numerical identifiers for statistical calculations. When the calculations are made, the implicit assumption is that a response of easy is equidistant from a view of very easy and difficult. Therefore,

Table 2. The surveyed topics ordered based on the interest ratings of the Midwestern university students. Items at the top of the table were viewed as more interesting than those listed at the bottom. Sample free statistics calculated for the survey indicate a reliability of 0.90. The raw averages were corrected for non-linearity, and each item's measurement error was calculated so that Figure 1 could be constructed and parametric tests utilized for analysis.

I	Topic	Count	Score	Raw Average	SD	Measure (Logits)	Error (Logits)
8	Glacial landforms	284	287	2.01	0.69	0.92	0.12
7	Mineral resources in the world	278	299	2.08	0.64	0.68	0.12
10	Way shorelines created	281	322	2.15	0.68	0.41	0.12
9	Role of wind in erosion	283	345	2.22	0.67	0.10	0.12
11	Identify minerals	283	350	2.24	0.80	0.01	0.12
13	Identify sedimentary rocks	283	357	2.26	0.78	-0.08	0.12
12	Identify igneous rocks	283	359	2.27	0.78	-0.11	0.12
14	Identify metamorphic rocks	282	360	2.28	0.78	-0.15	0.12
1	Difference between rocks and minerals	283	363	2.28	0.61	-0.17	0.12
6	Way metamorphic rocks form	285	366	2.28	0.67	-0.18	0.12
5	Way igneous rocks form	285	366	2.28	0.64	-0.18	0.12
3	Cross cutting for age	280	366	2.31	0.70	-0.26	0.12
15	Reading topographic maps	270	360	2.33	0.83	-0.28	0.12
4	Way sedimentary rocks form	284	378	2.33	0.64	-0.35	0.12
2	Rock cycle	284	378	2.33	0.68	-0.36	0.12

I = Survey item number as shown in Table 1.
Count = The number of respondents answering a survey item.
Score = The raw score calculated from all survey responses to a single item using the scale: 1 = very interesting; 2 = interesting; 3 = disinteresting; and 4 = very disinteresting.
Raw average = The arithmetic mean of the raw scores.
SD = The standard deviation of the raw score.
Measure = Item measure in logits.
Error = The standard error of the item measure in logits.

when the students complete this type of attitudinal survey, the numbers used to code the data imply an ordering of attitudes (5 is greater than 4, and 4 is greater than 3, etc.) but not a known spacing. Thorndike (1904) stressed the need to convert raw scores to measures, and Thurstone (1925, 1926) developed partial solutions to this measurement problem. However, not until the Rasch model was used by Wright and others did a technique for converting raw scores to measures become available. Item response theory can now be used to adjust non-linear rating scales (Andrich, 1982; Rost, 1988). The basic stochastic model used to convert raw scores of coded responses into true measures is discussed by Wright and Masters (1982), Rasch (1960), Andersen (1973, 1977), and Barndorff-Nielsen (1978).

Why use the Rasch model instead of factor analysis for these data? A complete discussion of this question would require a separate paper. Therefore, only a minimum number of theoretical and practical points are presented here. First, in factor analysis, ordinal scores are viewed as interval measures without error, while in Rasch analysis, ordinal responses are modeled as stochastic manifestations of linear parameters estimated with measurement error. Second, the use of the Rasch model enables irregular responses to be identified through fit statistics. With factor analysis, variance increases slightly as the result of irregular responses, but these irregular responses are not detectable from factors. Third, when factor analysis is utilized, the identification of solitary biased items is difficult. Bias eigenvalues are usually insignificant. The Rasch model, however, provides item fit statistics that allow poorly functioning items to be identified. Fourth, miskeyed items can cause problems in an analysis. In a factor analysis, eigenvalues which might highlight miskeys are usually insignificant. Misfit statistics from the Rasch model, however, can point to miskeyed items (see Wright (1991) for a discussion of the issues mentioned above). Finally, Duncan (1984, p. 206) made the following statement about the indeterminancy of factor analysis:

> The technology of factor analysis has to do with the estimation of the loadings from the observable correlations and the determination of the acceptability of the model, which is assessed by its ability to reproduce those correlations within the limits of sampling error. If the model is accepted, there is still an indeterminacy in the estimation of factor loadings inasmuch as systems of factors differing from those in $\rho_{12} = \sum_j \alpha_{1j}\alpha_{2j}$, but mathematically equivalent to them in the sense that they produce exactly the same correlations on the left-hand side (of the equation above), may be chosen in an infinity of ways.

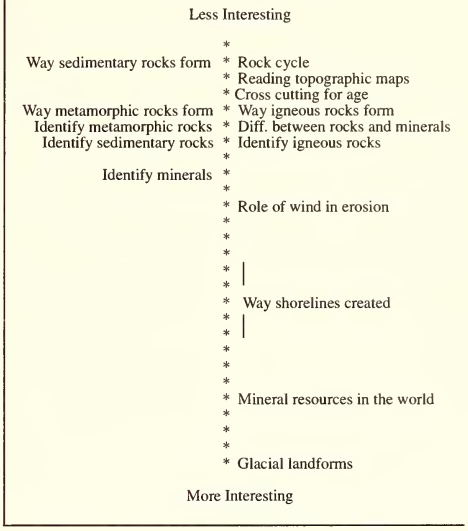
Discussions regarding the issues associated with factor analysis are provided by Reckase (1979), Abdullah (1989), and Raatz (1985).

The general relationship between logit values and raw scores can be seen by looking at the "Measure (Logits)" and "Raw Average" columns of Tables 2 and 3. The "Raw Average" column reports the average response of all survey takers to each item using the original coding. For the interest rating of topics, the coding scale was: 1 = very interesting; 2 = interesting; 3 = disinteresting; and 4 = very disinteresting. For the difficulty rating of topics, the coding scale was: 1 = very easy; 2 = easy; 3 = difficult; and 4 = very difficult. Thus, as Table 2 shows, the study of glacial landforms was rated on average as a 2.01 (on the 1-4 non-linear interest scale) by the students, indicating that, on average, the students not only found this topic interesting, but, of the surveyed topics, it was the most interesting. The difficulty of the same topic was rated as a 2.36 (on the 1-4 non-linear difficulty scale) by the students (Table 3), nearly halfway between easy and difficult, but, of the surveyed topics, the study of glacial landforms was viewed as one of the most difficult.

RESULTS

Data from the Midwestern University. The results of data analysis are shown in Tables 2 and 3 and Figures 1 and 2. In Figure 1, the item at the base of the thermometer, glacial landforms, was the most interesting class topic. The two items at the top of Figure 1, the way sedimentary rocks form and the rock cycle, were the least interesting class topics. Moving from the bottom of Figure 1 to its top, the items are rated according to decreasing interest. Figure 2 shows the survey items ranked on the difficulty scale. In this Figure, reading topographic maps appears at the top of the Figure, indicating that this topic was the most difficult, while the topic listed at the bottom of the Figure, the role of wind in erosion, was rated the least difficult.

Figure 1. A plot of the 15 Midwestern university class components as a function of item rating displayed on a linear scale corrected with the stochastic model. The standard error of all items was approximately that shown by the error bars for the topic, the way shorelines are created. Those items rated as more interesting are listed at the bottom of the chart, while those rated as less interesting are at the top. The full text of all items is given in Table 1.



Implications of Topics Ordered by Interest at the Midwestern University. Three topics were viewed as quite interesting: 1) the study of glacial landforms; 2) mineral resources; and 3) the creation of shorelines (Table 2 and Figure 1). One reason for their high rating might be that students feel familiar with these topics. Most students have seen pictures of mountains with alpine glaciers and have walked along a shoreline of some sort. Much of the geographic region from which this university attracts its students was affected by continental glaciation. Thus, many students are exposed to these concepts at some point in their pre-college education, even though they may not have taken an earth science course. The mineral resources of the world (i.e., searching for gold, silver, oil, etc.) might be interesting because students are generally familiar with mining, panning for gold, and oil exploration.

Four topics were clearly less interesting: 1) sedimentary rock formation; 2) determining the relative age of a rock; 3) the rock cycle; and 4) using topographic maps. The low interest level generated by age determination and using topographic maps might be related to the need to mentally translate a two-dimensional image into a three-dimensional one. Lectures and labs involving cross cutting usually ask the students to interpret a cross section in which a variety of igneous intrusions are present in order to determine the sequence in which geologic events took place. Their interpretation is further complicated by a fourth variable, time, which makes translating images from paper into three dimensions more difficult. Students may view topographic map reading as having no future use, or they may have difficulty in translating two-dimensional maps into

Table 3. The surveyed topics ordered based on the difficulty ratings of the Midwestern university students. Items at the top of the table were viewed as less difficult than those listed at the bottom. The sample free statistics calculated for the survey indicate a reliability of 0.93. The raw averages were corrected for non-linearity, and each item's measurement error was calculated so that Figure 2 could be constructed and parametric tests utilized for analysis.

I	Topic	Count	Score	Raw Average	SD	Measure (Logits)	Error (Logits)
9	Role of wind in erosion	282	312	2.11	0.53	0.56	0.12
6	Way metamorphic rocks form	283	323	2.14	0.55	0.41	0.12
4	Way sedimentary rocks form	282	323	2.15	0.52	0.40	0.12
1	Difference between rocks and minerals	280	324	2.16	0.63	0.34	0.12
5	Way igneous rocks form	281	327	2.16	0.51	0.33	0.12
7	Mineral resources in the world	280	329	2.18	0.54	0.27	0.12
2	Rock cycle	281	335	2.19	0.60	0.21	0.12
12	Identify igneous rocks	279	336	2.20	0.66	0.16	0.12
14	Identify metamorphic rocks	281	341	2.21	0.69	0.12	0.12
13	Identify sedimentary rocks	279	347	2.24	0.67	0.01	0.12
11	Identify minerals	277	355	2.28	0.72	-0.13	0.12
10	Way shorelines created	273	366	2.36	0.65	-0.45	0.11
3	Cross cutting for age	282	405	2.44	0.74	-0.71	0.11
15	Reading topographic maps	274	435	2.59	0.84	-1.16	0.11

I = Survey item number as shown in Table 1.
Count = The number of respondents answering a survey item.
Score = The raw score calculated from all survey responses to a single item using the scale: 1 = very easy; 2 = easy; 3 = difficult; and 4 = very difficult.
Raw average = The arithmetic mean of the raw scores.
SD = The standard deviation of the raw scores.
Measure = Item measure in logits.
Error = The standard error of the item measure in logits.

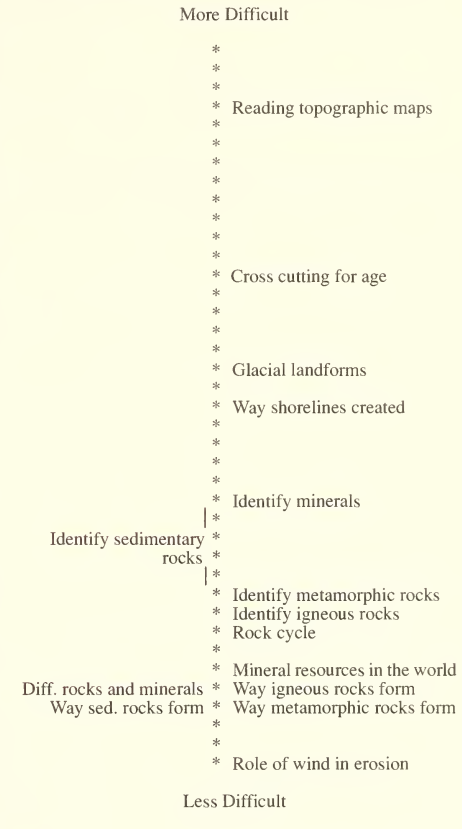
three-dimensional images. The rock cycle could have a low rating because the great length of time involved makes it difficult to visualize when compared to the human life span. The rock cycle is also hard to investigate in a laboratory setting.

Lectures and labs involving the way each rock type (i.e., igneous, sedimentary, and metamorphic) formed generated the same level of interest. Lectures and labs on sedimentary rock formation were rated lower than the labs and lectures involving igneous and metamorphic rock formation. Perhaps sedimentary rock formation is not as dramatic as igneous and metamorphic rock formation. Igneous rocks can be formed by volcanic activity, and metamorphic rocks can be formed when tectonic plates rub against each other. Sedimentary rock formation occurs when sediments are slowly carried into a region of deposition.

If sedimentary regions where substantial wave action occurs were discussed, the lectures and labs on this rock type might not have ranked so low.

Implications of Topics Rated by Difficulty at the Midwestern University. Figure 2 shows that the mineral identification lab was rated as more difficult than the lab on igneous rock identification. Since the mineral identification lab took place before any of the three rock identification labs, and since the ability to identify minerals helps in subsequent labs, the mineral identification lab *should* be more difficult than the igneous rock identification lab to which it contributes. The topic difficulty survey for lecture and lab also reveals another interesting result (Table 3 and Figure 2). The three lectures on rock formation are all rated at about the same difficulty level, but the labs for the identification of each rock type are rated as more difficult. This result seems predictable, since lectures involve listening, while labs involve an active doing, which is often more difficult.

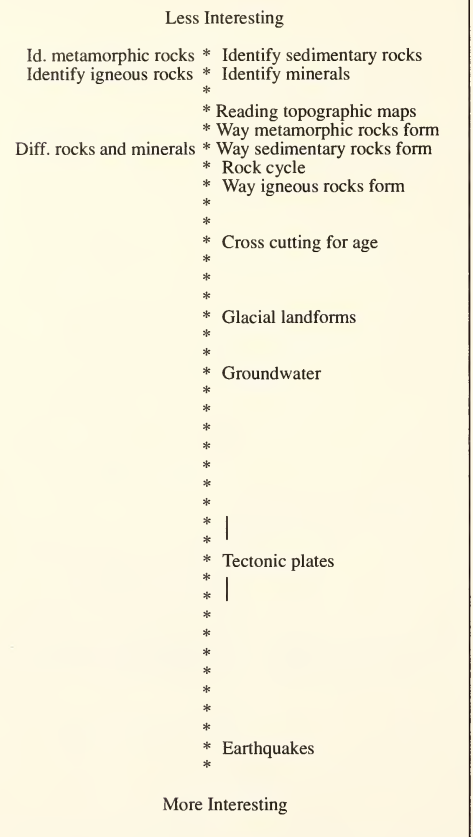
Figure 2. A plot of the 15 Midwestern university class components as a function of item rating displayed on a linear scale corrected with the stochastic model. The standard error of all items was approximately that shown by the error bars for the topic, identify sedimentary rocks. Those items rated as less difficult are listed at the bottom of the chart, while those rated as more difficult are at the top. The full text of all items is given in Table 1.



The high difficulty ratings of the labs for reading topographic maps, age determination, and glacial landforms may be a function of spatial visualization. In the case of glacial landforms, these features must be visualized and identified from two-dimensional maps and photographs, a skill which requires the ability to visualize two-dimensional data in three dimensions. Although shoreline creation is rated as less difficult than these three topics, it is also viewed as more difficult than the remaining eleven topics. Visualization is crucial for understanding the growth and deterioration of shorelines, because deposition along a shore can be a function of water depth. All of the surveyed topics call for some spatial visualization, but the skill level required for the more difficult topics may be higher than that required for other topics.

Rock formation, the differences between rocks and minerals, and the role of wind in erosion were considered far less difficult to understand than the other topics. These topics are simply definitive, while the other topics required the application of definitions and were, therefore, more difficult. At one time, each

Figure 3. A plot of the 15 Southern university class components as a function of item rating displayed on a linear scale corrected with the stochastic model. The standard error of all items was approximately that shown by the error bars for the topic, tectonic plates. Those items rated as more interesting are listed at the bottom of the chart, while those rated as less interesting are at the top. The error bars displayed in Figures 1 and 2 are smaller than those in Figures 3 and 4, because a smaller sample of students was available at the Southern university.



type of rock formation might have been viewed as difficult, but by the end of the course, these topics could have been considered relatively easy in comparison to other topics.

A qualitative comparison of Figures 1 and 2 provides added information with regard to the students' attitudes. Although glacial landforms and shoreline creation were viewed as quite interesting, these topics were not listed among the easiest topics by the students. Past experience might have helped the students maintain their interest in these difficult topics. Another explanation might be that a particular presentation technique made a difficult topic more interesting (e.g., very good slides or actively involving the students in the lecture).

The two most difficult topics were also of low interest (i.e., topographic maps and age determination). Predictably, some highly difficult topics might be viewed as not very interesting. Follow-up interviews might reveal if the difficulty of these two topics caused students to view them as uninteresting or if the students lacked interest for other reasons. In the future, students could be randomly selected and interviewed at the end of the course.

Topic Difficulty at Both Institutions. The laboratory identification of rocks and minerals was rated as relatively difficult in comparison to the other topics at both schools (Figures 1 and 3). Furthermore, the ratings for the three rock identification labs at both schools are all clustered together with no clear statistical difference between the sets of labs. Topographic map reading was considered relatively difficult at both institutions. One topic that was rated very differently at the two schools was age determination. Cross cutting relationships were rated as easy at the Southern university (Tables 5 and 6), and this item was also rated fairly high in terms of interest. These results are in marked contrast to what was found at the Midwestern university (i.e., a high difficulty and low interest rating for age determination). A review of course syllabi and discussions with the instructors suggested that the difference was probably related to the complexity of the

Table 4. The list of topics surveyed at a Southern university. Topics 11-15 were labs. One survey asked students to indicate their level of interest for each of the topics by choosing from four possible responses: 1) very disinteresting; 2) disinteresting; 3) interesting; and 4) very interesting. A second survey asked students to indicate how difficult each topic was to understand by selecting from four possible responses: 1) very difficult; 2) difficult; 3) easy; and 4) very easy. The topics presented to students at the second institution are provided in Figures 3 and 4.

1	The difference between rocks and minerals
2	The rock cycle
3	Using cross-cutting relationships to determine the relative age of rocks
4	The way sedimentary rocks are formed
5	The way igneous rocks are formed
6	The way metamorphic rocks are formed
7	Earthquake distribution and occurrence
8	Tectonic plate movement and location
9	Groundwater issues
10	Glacial landforms
11	Identifying minerals
12	Identifying igneous rocks
13	Identifying sedimentary rocks
14	Identifying metamorphic rocks
15	Reading topographic maps

cross-cutting problems posed to students. Simpler cross-cutting scenarios requiring less spatial visualization were used at the Southern university.

The different ratings for the rock cycle is probably related to the presentations used in the two universities. The Midwestern students, who rated the topic as being more difficult (in comparison to the other rated topics), spent a greater amount of lecture time studying the rock cycle. As a result, material of greater complexity was covered. At the second institution, a less-detailed look at the rock cycle was presented. Although differences exist in the relative rating of the rock cycle to other topics at the two institutions, the students rated the rock cycle as easy at both schools.

Interest. The interest data collected from students at both institutions reveals some similar trends across institutions as well as some differences (Figures 2 and 4). At both schools, the labs requiring the identification of rocks and minerals were clumped together based on their interest ratings. The average ratings for these labs at the Midwestern university indicated interest in the labs (Table 2), but the ratings from the Southern university suggested that the students were not interested in these labs (Table 5). A review of the syllabi and topic development in each course suggests that these labs were rated higher at the Midwestern university as a result of over 20 years of course development by the instructor, while the labs at the second university had not been used for nearly as long.

Table 5. The surveyed topics ordered based on the interest ratings of the Southern university students. Items at the top of the table were viewed as more interesting than those listed at the bottom. The sample free statistics calculated for the survey indicate a reliability of 0.90. The raw averages were corrected for non-linearity, and each item's measurement error was calculated so that Figure 3 could be constructed and parametric tests utilized for analysis.

I	Topic	Count	Score	Raw Average	SD	Measure (Logits)	Error (Logits)
7	Earthquakes	52	90	1.75	0.67	2.82	0.28
8	Tectonic plates	52	104	2.07	0.76	1.75	0.27
9	Groundwater	52	118	2.34	0.86	0.79	0.25
10	Glacial landforms	51	120	2.36	0.78	0.52	0.25
3	Cross cutting for age	52	130	2.50	0.76	0.06	0.24
5	Way igneous rocks form	51	132	2.60	0.74	-0.16	0.24
2	Rock cycle	51	134	2.67	0.79	-0.32	0.24
1	Difference between rocks and minerals	52	137	2.68	0.72	-0.35	0.24
4	Way sedimentary rocks form	52	137	2.64	0.70	-0.35	0.24
6	Way metamorphic rocks form	52	139	2.68	0.72	-0.47	0.24
15	Reading topographic maps	52	142	2.75	0.98	-0.64	0.24
11	Identify minerals	52	146	2.82	0.90	-0.87	0.24
12	Identify igneous rocks	52	147	2.84	0.89	-0.93	0.24
13	Identify sedimentary rocks	52	147	2.84	0.89	-0.93	0.24
14	Identify metamorphic rocks	52	147	2.84	0.87	-0.93	0.24

I = Survey item number as used in Table 4.
Count = The number of respondents answering a survey item.
Score = The raw score calculated from all survey responses to a single item using the scale: 1 = very interesting; 2 = interesting; 3 = disinteresting; and 4 = very disinteresting.
Raw average = The arithmetic mean of the raw scores.
SD = The standard deviation of the raw score.
Measure = Item measure in logits.
Error = The standard error of the item measure in logits.

Student interest at both schools was similar in other ways (Figures 1 and 3). For example, topics that the students had some experience with (e.g., running along a shoreline) and/or that were timely (e.g., a major earthquake) were often highly rated. At the Southern university, the sessions on earthquakes, tectonic plates, groundwater, and glaciers were all highly rated, but topographic maps were less interesting.

The topic of groundwater caused some unexpected idiosyncratic responses from the Southern university. Although the students, on average, rated this topic as *interesting*, when all of their responses were reviewed, a number of unexpected *very interesting* ratings were found. This result might indicate a situation that is the opposite of what was observed for topographic maps. At the South-

Table 6. The surveyed topics ordered based on the difficulty ratings of the Southern university students. Items at the top of the table were viewed as less difficult than those listed at the bottom. The sample free statistics calculated for the survey indicate a reliability of 0.93. The raw averages were corrected for non-linearity, and each item's measurement error was calculated so that Figure 4 could be constructed and parametric tests utilized for analysis.

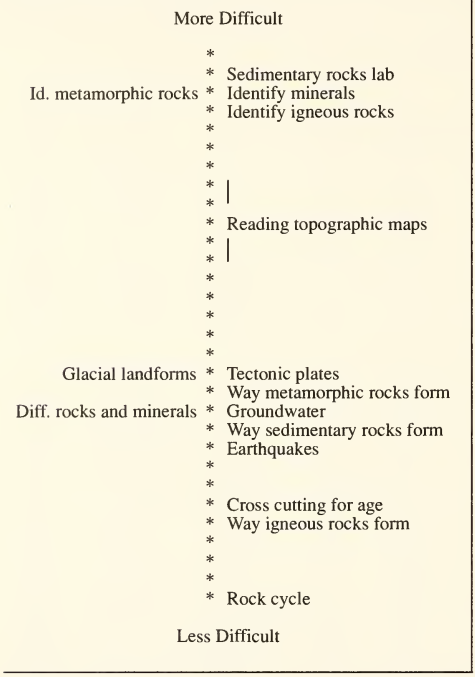
I	Topic	Count	Score	Raw Average	SD	Measure (Logits)	Error (Logits)
2	Rock cycle	55	103	1.87	0.55	1.48	0.28
5	Way igneous rocks form	55	109	1.98	056	1.06	0.27
3	Cross cutting for age	55	110	2.00	0.58	0.93	0.27
7	Earthquakes	56	116	2.07	0.66	0.65	0.26
4	Way sedimentary rocks form	56	118	2.11	0.53	0.51	0.26
1	Difference between rocks and minerals	54	116	2.15	0.63	0.38	0.26
9	Groundwater	56	120	2.14	0.55	0.38	0.25
6	Way metamorphic rocks form	56	121	2.16	0.60	0.31	0.25
10	Glacial landforms	55	120	2.18	0.58	0.23	0.25
8	Tectonic plates	56	123	2.20	0.59	0.18	0.25
15	Reading topographic maps	56	137	2.45	0.87	-0.63	0.23
12	Identify igneous rocks	54	145	2.69	0.84	-1.24	0.22
14	Identify metamorphic rocks	55	150	2.73	0.83	-1.39	0.22
11	Identify minerals	55	150	2.73	0.76	-1.39	0.22
13	Identify sedimentary rocks	55	151	2.75	0.84	-1.44	0.22

I = Survey item number as used in Table 4.
Count = The number of respondents answering a survey item.
Score = The raw score calculated from all survey responses to a single item using the scale: 1 = very easy; 2 = easy; 3 = difficult; and 4 = very difficult.
Raw average = The arithmetic mean of the raw scores.
SD = The standard deviation of the raw score.
Measure = Item measure in logits.
Error = The standard error of the item measure in logits.

ern university, the topic of groundwater was more relevant to the students' real-life experiences than other topics. The instructor said that this particular topic was one which stressed the impact of pollution on groundwater. Also, the issue of groundwater had been a hot political topic in their State.

A comparison of the ratings at the two institutions shows some important similarities as well as some differences. The structure of the class, the experience of the instructor, and the training of the graduate assistants who lead lab sections are all factors that help shape a student's reaction to geology. Although these factors will always remain influential, some particular trends in student attitude were observed across these two schools. Labs generated relatively little interest, but topics that are in the news or that have been experienced by the students are of greater interest than subjects that are less tangible. Finally, at both

Figure 4. A plot of the 15 Southern university class components as a function of item rating displayed on a linear scale corrected with the stochastic model. The standard error of all items was approximately that shown by the error bars for the topic, reading topographic maps. Those items rated as less difficult are listed at the bottom of the chart, while those rated as more difficult are at the top.



schools, student interest in labs and lectures did not differ as a function of rock type taught (i.e., lessons involving igneous, sedimentary, and metamorphic rock).

CONCLUSION

Many plausible reasons exist which might explain the ratings discussed in this paper. Some of these factors are text presentation, the teacher, student attendance, and recent lecture topics. Despite all of these uncontrollable variables, a survey of students' views toward earth science topics reveals some interesting trends and patterns which may be helpful to earth science teachers at all levels and which may provide information for researchers exploring attitudes toward science. Two keys to understanding the ratings appear to be: 1) familiarity with a topic; and 2) the anxiety arising from using spatial visualization for the first time. The topics of greatest interest seem to be those that are in the news, timely, and/or dramatic.

Although the instructors and topics varied, some general trends were observed across institutions. The relatively low interest ratings of the rock identification labs at both schools suggests that the organization of the labs might be changed. Hopefully, doing a lab should be more interesting than passively listening to a lecture. The highly rated topics at both schools seem to be those with which the students can relate. Instructors should try to relate topics to their students' lives and experiences. By doing so, the students' interest may increase. This suggestion might seem to be common sense, but it must be practiced in college science classes. Certainly, a constructivist philosophy of teaching would support this goal (Fraser, 1994).

The results of this study demonstrate that detailed attitudinal data regarding geology topics can be collected, evaluated with a probabilistic model, and used to help instructors understand student perceptions. Whatever the earth science course, this type of analysis can be used to refine courses, ultimately increasing the students' interest and understanding as well as expanding the data base of research on earth science education.

A review of course syllabi, texts, labs, and teaching techniques helps explain how course structure and teaching strategies may have affected topic ratings.

Both instructors lectured to large groups of students, and only a small amount of time was devoted to question and answer. Both instructors used overhead transparencies, board work, and slides.

For these instructors, topics that were tied to a current issue, connected to students' interest, and/or presented in a wide variety of ways were the topics rated as the most interesting. The use of slides, which build upon textbook photos, and simple diagrams seem to decrease difficulty and to increase interest. The instructor at the Southern university felt that his explanation of igneous rock formation was successful because he related the topic to ice cubes melting and forming. He also talked at great length about crystals, such as sugar, dissolving in water when discussing melting.

The instructors and researcher felt that low-rated topics resulted from a lack of analogies, a lack of suitable tie-ins to real life, and, perhaps, to excessive detail when a topic in their particular area of expertise was covered. The instructor at the Southern school felt that the students' view of metamorphic rock formation being more difficult to understand than the formation of other rock types resulted from his use of phase diagrams while discussing the formation of metamorphic rocks. The phase diagrams confused the class. The same instructor also spent a great deal of time talking about stable and unstable minerals. Because no suitable examples were available, the students also found this material confusing.

Another issue was the way the instructors thought students should apply lecture and textbook information in lab. For example, a wide range of techniques that could be used to identify rocks and minerals were presented in lecture and lab. Even though the necessary supplies and reagents were provided to the students, the undergraduates completed the rock and mineral labs by simply memorizing the appearance of the samples.

The collection of attitudinal data from earth science students can provide far-ranging information that is of use to course instructors. The attitudes of the students are easy to evaluate and consider. Since little research has been carried out on earth science classes, almost any study will provide new, publishable information for scientists and science educators. The results of this analysis show that some earth science topics are more interesting to non-majors than others. Since an appreciation (and understanding) of science is so important for all students, this type of study can provide very important information that can be used to improve lab-based science courses.

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POST-CONFLICT BEHAVIOR IN JAPANESE MACAQUES AT THE INDIANAPOLIS ZOO: AGE OF OPPONENTS INFLUENCES RECONCILIATION

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ABSTRACT: In many primate species, opponents may affiliate soon after an agonistic encounter. This study examined how the individual characteristics of opponents affected post-conflict interactions in a captive group of Japanese macaques (*Macaca fuscata*). Reconciliation and selective attraction of opponents was shown to occur following agonistic encounters. The factor most strongly influencing post-conflict interactions was age. Juveniles were significantly more likely than adults to initiate reconciliation. Sex, kinship, and dominance status were not associated with contact initiation. Because juveniles were the most likely victims of aggression, juvenile reconciliatory contact initiative may reduce the threat of further aggression.

KEYWORDS: Age, aggression, conflict, Japanese macaque, primate, reconciliation, social behavior.

INTRODUCTION

In many primate species, opponents may attempt to reaffiliate soon after the agonistic encounter (de Waal, 1989). De Waal and van Roosmalen (1979) interpreted such behavior as reconciliation. De Waal and Yoshihara (1983) developed a controlled method to quantify this behavior. Whereas their null hypothesis predicts random interaction of opponents following a conflict, two alternative hypotheses predict either post-conflict avoidance (dispersal) or attraction (reconciliation). Chimpanzees (de Waal and van Roosmalen, 1979), bonobos (de Waal, 1987), patas monkeys (York and Rowell, 1988), golden monkeys (Ren, *et al.*, 1991), redfronted lemurs (Kappeler, 1993), and several macaque species (de Waal and Yoshihara, 1983; Judge, 1983; Thierry, 1984: Cords, 1988; de Waal and Ren, 1988; Aureli, *et al.*, 1989) are known to exhibit reconciliatory behavior.

Either the aggressor or the victim may initiate post-conflict affiliation. In rhesus macaques, post-conflict affiliation is most often initiated by the aggressor (de Waal and Luttrell, 1989), whereas among pigtail macaques, the victim initiates this behavior (Judge, 1991). Questions regarding contact initiation, however, must also be addressed from a multi-component perspective, because different factors may interact to produce unique behavior. For example, age and

sex might influence which opponent makes initial contact. Aureli, *et al.* (1989) found that within a troop of long-tailed macaques, the victim most often sought reconciliation, whereas Cords (1988) found that in an isolated group of immature male long-tailed macaques, the aggressor did so. Kinship might also influence reconciliation, but several studies have shown either no differential reconciliation among kin (Aureli and van Schaik, 1991a; Aureli, *et al.*, 1994) or kin-oriented reconciliation that was a consequence of the elevated affiliative behavior generally found among kin (Cheney and Seyfarth, 1989).

Because combinations of attributes vary among group members, one might expect individuals to express different reconciliatory behavior depending on factors such as sex, age, relatedness, dominance rank, or reproductive condition, especially if difference in these factors influence the value of a relationship between a pair of individuals (see Cords and Thurnheer (1993) for a discussion of social value and reconciliation). This study was designed to quantify reconciliation in a captive group of Japanese macaques (*Macaca fuscata*), taking into account characteristics such as the sex, age, kinship, and dominance status of the opponents. While other studies have examined reconciliation in this species (Friedlen and Chaffin, 1991; Aureli, *et al.*, 1993), none have reported on whether such factors influence post-conflict interactions between opponents.

MATERIALS AND METHODS

The Study Group. A captive group of 15 Japanese macaques was observed from June to August 1992 at the Indianapolis Zoo. The group, established at least two years prior to the study, consisted of one adult male (AM; > 5 years), six adult females (AF; > 5 years), two juvenile males (JM; 1-4 years), four juvenile females (JF; 1-4 years), and two infants (I; < 1 year). Kin relationships (hyphenated) and descending matrilineal dominance rank were as follows: AM1; AF1-JF1-JM1; AF2-JF2-JF3; AF3-JF4-I1; AF4; AF5-JM2-I2; and AF6. No adults were related. During the day, the group inhabited an outdoor enclosure with adequate room to run and climb (167 m^2). Behavioral observations were made only on days that were at least partly sunny from 10:00 until the animals were fed at 16:00.

Data Collection. Observational procedures were similar to those used by de Waal and Yoshihara (1983; but see Kappeler and van Schaik (1992) for a discussion of methodological concerns). Immediately following a spontaneous agonistic encounter, one of the opponents was selected at random and observed for a 10-minute focal period (post-conflict observation). Agonistic conflict was defined as an interaction that included lunging or chasing, accompanied by eye-flashing or certain vocalizations (i.e., screaming directed toward the opponent). On the next observation day, the same individual was watched for 10 minutes, beginning at the same time that the agonistic encounter had ended on the previous day (matched control observation). The matched control observation was postponed until the next day if the focal animal participated in an agonistic conflict immediately prior to or during the first minute of the focal period.

Data were recorded on a hand-held computer and included the following: identity of the opponents, minute block in which contact with the other individuals occurred, identity of contact partners, identity of contact initiators , and specific behavioral patterns (chase, vocalize, eye-flash, hit, bite, sit-near, touch, groom, mount, move-away).

Opponent pairs were classified as either attracted, dispersed, or neutral, according to the definitions of de Waal and Yoshihara (1983). Attracted pairs were those in which non-agonistic contact (touching or sitting within arm's reach for more than 10 seconds) occurred only during post-conflict observation or earlier in the post-conflict than in the matched control observations. These pairs were designated as reconciliatory. Dispersed pairs showed the opposite configuration (i.e., contact in the matched control observations only or earlier in the matched control than in the post-conflict observations). Neutral pairs made no contact at all or made contact in the same minute block in both the post-conflict and matched control observations.

For the purposes of this study, the behavior of the infants was not recorded. Also, because this study was primarily concerned with interactions between individuals, solitary behaviors such as self-grooming or foraging were not recorded.

Data, unless otherwise indicated, were analyzed using two-tailed nonparametric procedures (Siegel and Castellan, 1988) to avoid making the stringent assumptions generally associated with parametric statistics. To avoid the statistical error associated with the pooling of data across individuals, χ^2 procedures were not used. Therefore, unless otherwise indicated, sample size was 13 with $\alpha = 0.05$.

RESULTS

One hundred two post-conflict and corresponding matched control observations were conducted. Because conflicts were sometimes triadic or polyadic, a total of 131 matched opponent pairs was observed. In the analyses of opponent characteristics, frequencies of attraction or dispersal for a given individual were treated as proportions of the total number of conflicts in which that individual was paired.

Overall Occurrence of Reconciliatory Behavior. Post-conflict interactions between opponents generally involved an individual approaching to sit in contact or within arm's reach of a former opponent. While this behavior sometimes resulted in renewed aggression (such instances were dropped from the analysis), most often the two opponents remained seated together for at least 10 seconds. On many occasions, this contact immediately led to a grooming bout. Reconciliation between juveniles, particularly the young males, often involved play behavior.

The null hypothesis predicted equal frequencies of attraction and dispersal. The results of the present study, however, revealed that individuals were significantly more likely to show attraction than dispersal (Figure 1; Wilcoxon Signed Rank Test: T+ = 77, T- = -14, and $P = 0.0303$). When the frequencies of

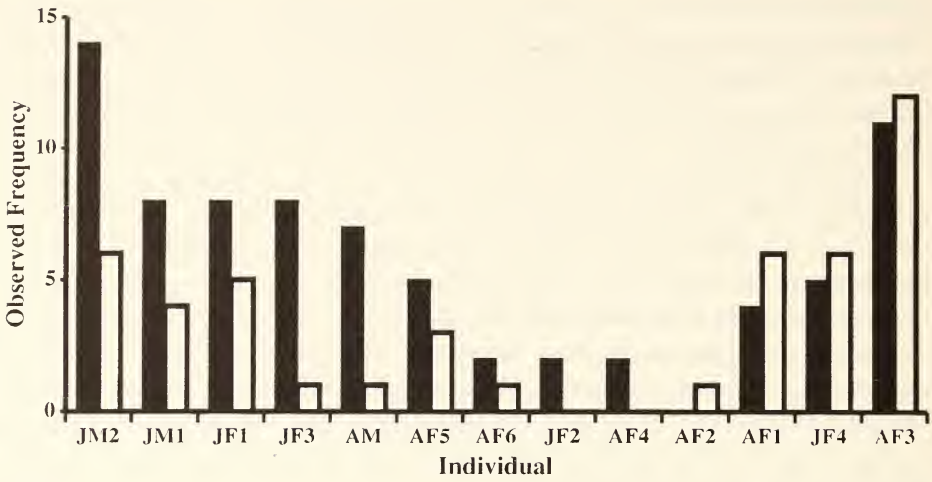

Figure 1. The number of times each individual appeared in attracted (shaded bar) or dispersed (clear bar) pairs (A = adult; J = juvenile; M = male; F = female; Wilcoxon Signed Rank Test, $P = 0.0303$).

attraction and dispersal are expressed as proportions of the total interactions per individual, the difference was reduced to a strong trend (Wilcoxon Signed Rank Test: T+ = 73, T- = -18, $P = 0.06$).

De Waal and Yoshihara (1983) stressed the importance of distinguishing between actual reconciliation and a general increase in contact following an agonistic encounter. Their concern was addressed by comparing the proportion of non-agonistic contacts between opponents and between the focal animal and all other individuals in both post-conflict and matched control observations. Focal animals made significantly more contacts with opponents relative to all other individuals during post-conflict rather than during matched control observations (Figure 2; Wilcoxon Signed Rank Test, 2 zero scores: T+ = 56, T- = -10, $P = 0.0454$). These Japanese macaques, therefore, exhibited selective post-conflict attraction for opponents.

Aggressors and victims displayed no difference in contact initiative (active approach and solicitation) following a conflict (Wilcoxon Signed Rank Test, 6 zero scores: T+ = 19.5, T- = -8.5, $P = 0.3980$). Contact initiative was attributed to the opponent who first approached and sat at least within arm's length of the other for more than 10 seconds.

Opponent Characteristics. Among individuals, differences in attraction with respect to opponent sex approached significance (male:male vs. male:female vs. female:female; Kruskal-Wallis, $P = 0.065$). In opposite sex pairs, the trend was for males, more than females, to be the contact initiator (Wilcoxon-Mann-Whitney Test, one-tailed, $P = 0.0917$). In general, however, sex was not a significant factor influencing reconciliation. Males and females did not differ in frequencies of attracted and dispersed interactions (Wilcoxon-Mann-Whitney

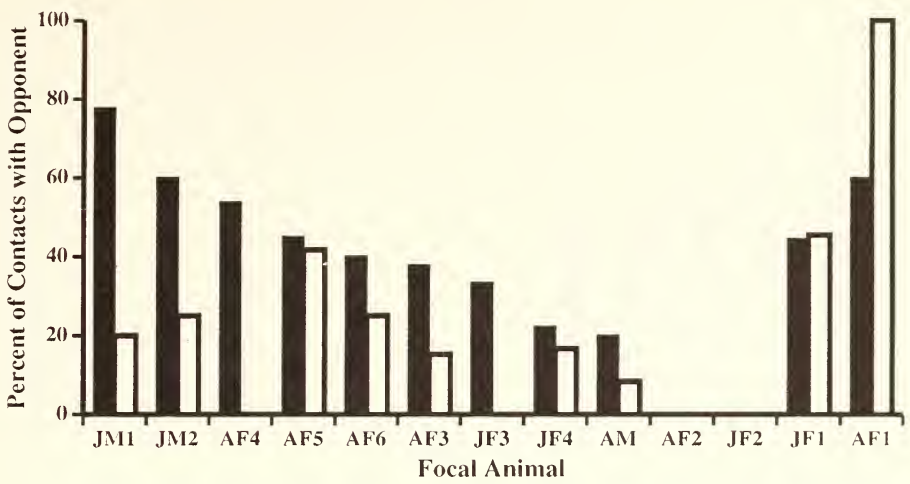

Figure 2. The proportion of a focal animal's total contacts that involved the opponent during post-conflict (shaded bar) and matched control (clear bar) observations (A = adult; J = juvenile; M = male; F = female; Wilcoxon Signed Rank Test, $P = 0.0454$).

Test, $P = 0.2049$) nor were members of either sex more likely, in general, to be contact initiators (Wilcoxon-Mann-Whitney Test, $P = 0.2719$).

Dominance status and the kinship of opponents also had no detectable effect on which individual initiated post-conflict interactions. Whether an individual was more or less dominant than its opponent did not influence contact initiation (Wilcoxon Signed Rank Test, 5 zero scores: T+ = 21, T- = -15, $P = 0.7263$). Likewise, relatedness of opponent did not influence whether an individual initiated reconciliation (Wilcoxon Signed Rank Test, N = 10, 3 zero scores: T+ = 9, T- = -19, $P = 0.4469$). Individuals with no kin were excluded from the analysis. Note that no matrilines contained more than one adult female, simplifying the application of kinship and dominance data.

Of the factors analyzed, the age of the opponents appeared to have the strongest influence on reconciliation. Regardless of age, aggressors were more likely to attack juveniles than to attack adults (Wilcoxon Signed Rank Test, 2 zero scores: T+ = 59, T- = -7, $P = 0.0234$). Juveniles were significantly more likely than adults to be contact initiators (Figure 3; Wilcoxon-Mann-Whitney Test, $P = 0.0321$). There were also significant reconciliatory differences among individuals with respect to the age of the opponent (adult:adult vs. adult:juvenile vs. juvenile: juvenile; Kruskal-Wallis, $P = 0.0344$) with juvenile:juvenile pairs more likely to be attracted than adult:adult pairs (Multiple Comparisons, $P < 0.05$).

DISCUSSION

Although zoo personnel have attempted to simulate natural conditions for this group of macaques, restricted space, small group size, and human presence necessitate caution when relating the findings of this study to wild populations.

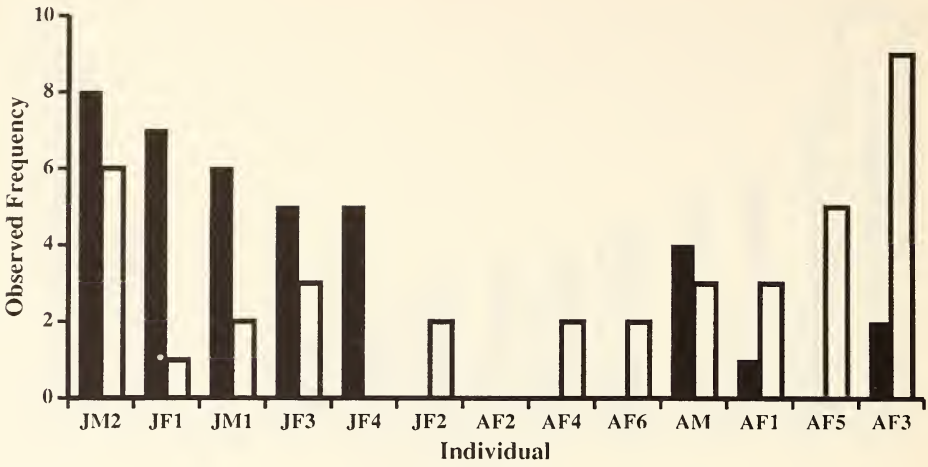

Figure 3. The number of times each individual was an active contact initiator following a conflict (shaded bar) and a passive contact (clear bar) recipient (A = adult; J = juvenile; M = male; F = female; Wilcoxon-Mann-Whitney Test, $P = 0.0321$).

Nevertheless, some general tendencies are apparent regarding the social behavior of Japanese macaques in captivity.

Selective attraction, as defined by de Waal and Yoshihara (1983), involves both an absolute and relative increase in post-conflict affiliation between opponents. This occurred in the captive Japanese macaque troops studied by Friedlen and Chaffin (1991) and Aureli, *et al.* (1993) as well as in the Indianapolis group discussed here. The Japanese macaque is part of a growing list of primate species in which such reconciliatory behavior occurs. Contact between opponents following a conflict is thought to function not only in the repair of social relationships (de Waal and van Roosmalen, 1979) but also in the maintenance of group cohesion (de Waal, 1986) and in the reduction of acute stress in victims of aggression (Aureli, *et al.*, 1989; Aureli and van Schaik, 1991b). The prevalence of reconciliation among primate groups has prompted de Waal (1986, 1987) to call for its inclusion as a fundamental concept in the study of social dominance.

Although sex, dominance status, and kinship of opponents did not influence reconciliation, the age of opponents played an important role in post-conflict interactions. Juveniles were the individuals most likely to initiate contact following an aggressive encounter. Adults almost never actively reconciled conflicts involving juveniles. Perhaps juveniles benefit from affiliative post-conflict interactions more than adults. In this study, aggression between individuals of differing age classes was directed almost entirely toward juveniles. Therefore, juveniles should be more likely to initiate reconciliation if such behavior diminishes the threat of aggression from an adult. Other studies support this hypothesis: long-tailed macaques exhibit a decreased frequency of displacement behavior following allogrooming (Schino, *et al.*, 1988) and the threat of future aggression

appeared to diminish among pigtail macaques following reconciliation (Judge, 1983). However, other studies have offered only weak support for this trend (Aureli, *et al.*, 1989).

The occurrence of defensive coalitions could partly explain the age bias in reconciliation behavior. Kurland (1977) found that adult Japanese macaques often came to the defense of juveniles that were victims of aggression, thereby halting further aggression. Although this type of coalition was most common among related females, other individuals, particularly the dominant male, often defended non-relatives. This observation suggests that juveniles should actively solicit reconciliation with adults, as such action could secure valuable allies in future conflicts.

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BATS OF ABANDONED COAL MINES IN SOUTHWESTERN INDIANA

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ABSTRACT: Double-frame harp bat traps were used to sample the bats at the entrances to 26 abandoned coal mines in ten Indiana Counties between 1984 and 1995. A total of 49 samples was collected. A total of 204 bats was captured, including 84 eastern pipistrelles *(Pipistrellus subflavus;* a mean of 1.4 per visit), 80 northern myotis *(Myotis septentrionalis;* a mean of 1.7 per visit), 39 little brown myotis (*M. lucifugus*; a mean of 0.8 per visit), and 1 big brown bat *(Eptesicus fuscus;* a mean of 0.02 per visit). Most samples yielded few or no bats. Only five samples yielded more than 3 bats. (Three samples at two entrances at a new site after this paper had been completed yielded 88 additional bats, including 2 male Indiana myotis, a Federally endangered species.)

KEYWORDS: Bats, bat roosts, coal mines, *Eptesicus*, hibernacula, *Myotis*, *Pipistrellus*.

INTRODUCTION

Coal was first discovered in Indiana along the Wabash River in 1736. Underground coal mining began in the State in the mid-1800s. As a consequence, abandoned underground coal mines underlay extensive areas of southwestern Indiana. Many of the shafts and portals at these old mines remained open when mining ceased, sometimes posing extreme public health and safety hazards to humans and other animals.

The Indiana Department of Natural Resources, Division of Reclamation's Restoration Program administers the Abandoned Mine Land Program that reclaims areas disturbed by coal mining prior to 1977. The purpose of reclamation at these sites is to reduce if not eliminate health, safety, and environmental hazards, while improving productivity and enhancing the esthetics of the landscape. To date, the Indiana Abandoned Mine Land Program has sealed nearly 300 shafts and portals.

All of the species of bats in Indiana that traditionally use caves for roosting, hibernating, or reproducing will use mines for these purposes. Some of the species of bats that might use these old mines are listed as State or Federally endangered and are, therefore, in need of protection. The Indiana Abandoned Mine Land Program is consequently required to assess these mines for use by bats prior to

reclamation and cannot destroy the habitat if Federally endangered species are found. The alternative is typically to install a "bat gate" at the entrance of the mine that prevents human entrance but still allows bats to enter and exit the mine unencumbered.

Twelve species of bats are (or recently were) known from Indiana and nine species typically use caves or mines (Mumford and Whitaker, 1982). However, the southeastern myotis (*M. austroriparius*) has not been documented in the State since 1970, and the big-eared bat (*Plecotus rafinesquii*) has not been documented since 1962. Both are considered extirpated. The following seven species currently hibernate in caves in Indiana: the little brown myotis (*Myotis lucifugus*), the Indiana myotis (*M. sodalis*), the northern myotis (*M. septentrionalis*), the gray myotis (*M. grisescens*), the big brown bat (*Eptesicus fuscus*), and the eastern pipistrelle (*Pipistrellus subflavus*). The silver-haired bat (*Lasionycteris noctivagans*) occasionally hibernates in caves or mines.

Among the bats found in Indiana, two are on the United States Fish and Wildlife Service's Endangered and Threatened Wildlife and Plants list. One, the gray myotis, is the only bat currently present in Indiana that forms maternity colonies in caves or mines. The only nursery colony of that species known in Indiana was located in 1982 (Brack, *et al.*, 1984b) in Clark County. The other Federally endangered species, the Indiana myotis, uses caves or mines for hibernation and for swarming (Brack, *et al.*, 1984a; Cope and Humphrey, 1977; Mumford and Whitaker, 1982). Male gray and Indiana myotis as well as bats of other species sometimes roost in caves in summer. The Indiana Department of Natural Resources, Division of Fish and Wildlife, considers all Federally listed species as endangered in Indiana. The evening bat (*Nycticeius humeralis*) is considered state endangered in Indiana, but it does not enter caves.

Since 1984, Indiana Division of Reclamation has funded field assessment of sites that might serve as roosts for bats. Some of these sites consist of buildings and other structures, but 26 of them contained one or more open mine entrances. The purpose of this paper is to report on bats using these entrances.

MATERIALS AND METHODS

The 26 sites were sampled a total of 49 times between 1984 and 1995, using a double-frame harp bat trap at one or more entrances. The trap was usually tended from dusk to midnight or later on one or more visits (usually 1-3). The trap was placed at the entrance to the mine, and bird netting was used around the trap to prevent bats from entering or exiting without passing through the trap. A bat detector was used to monitor bat activity in the vicinity of the entrance while the trap was in operation. The detector allowed determination of whether there were bats in the area and of the trap success relative to the number of bat calls heard. All bats were identified, their sex was checked, and they were released. Twenty-six sites were sampled in ten Indiana Counties (Table 1).

Most of the entrances were horizontal, but a few were vertical. The mines were not explored because of the danger, but the mines sampled were all those

Table 1. Bats captured in bat traps at abandoned coal mines in southwestern Indiana.

County	Number of mines Sampled	Number of mines with Bats	Number of Visits to Mines	*Pipistrellus subflavus*	*Myotis septentrionalis*	*Myotis lucifugus*	*Eptesicus fuscus*	Total Bats
Clay	7	5	18	54	47	27	1	129
Greene	2	1	4	1	0	0	0	1
Martin	1	1	1	0	1	0	0	1
Owen	1	0	3	0	0	0	0	0
Parke	3	2	5	8	9	2	0	19
Pike	2	2	2	19	21	10	0	50
Spencer	1	0	3	0	0	0	0	0
Sullivan	4	1	7	2	0	0	0	2
Warrick	3	0	3	0	0	0	0	0
Vigo	2	1	3	0	2	0	0	2
Totals	26	13	49	84	80	39	1	204

that appeared from the entrance to have any potential of having internal passageways that might make them suitable as bat roosts.

The most likely time to find activity at mine entrances is from late August through late October, when bats tend to gather or "swarm" at cave and mine entrances presumably for mating and/or hibernacula assessment purposes. Bats may emerge in spring from caves or mines serving as hibernacula, but bat activity at this time of year is usually less. Therefore, most of our sampling occurred in late summer and fall, but some sampling was carried out in spring and early summer. The only bats of Indiana likely to use caves or mines as maternity colonies are the southeastern myotis (probably extirpated) and the gray bat (not likely in southwestern Indiana).

RESULTS

Four species of bats totaling 204 individuals were captured at the 26 mine entrances in 49 visits (mean of 4.2 per visit). This included 84 eastern pipistrelles (1.7 per visit), 80 northern myotis (1.6 per visit), 39 little brown myotis (0.8 per visit), and 1 big brown bat (0.02 per visit). No bats at all were taken at 13 (50%) of the entrances; only one bat was taken at each of five entrances; two were taken at each of three entrances; and 3 bats were taken at one entrance. In only five (19.2%) of the sites were more than three bats taken: 34 in one visit to site 20, 26 in one visit to site 174, and 65 in six visits to site 423 in Clay County; 50 in one visit to site 228 in Pike County; and 18 in two visits to site 651 in Parke County. (The site locations are on file with the Division of Reclamation.)

DISCUSSION

Surprisingly few of the abandoned mines in southwestern Indiana were regularly visited by bats. Nothing special was noted in those mines that contained the larger numbers of bats. Perhaps conditions differed considerably inside the

mines. Several non-endangered bat species utilize underground coal mines in Indiana, but no endangered species were found to do so. Consequently, the Indiana Abandoned Mine Land Program has not been required to install bat gates. However, many or most of the bat species in the State are probably declining due to loss of habitat. The Division of Reclamation has come to realize the importance of protecting bat habitat, even if no endangered bats are currently using it. The installation of bat gates, especially in remote, rugged areas, appears to be both economically feasible and less environmentally disturbing than traditional methods of sealing mine entrances. Therefore, the Division of Reclamation is currently considering installing bat gates at five reclamation projects to protect bats and bat habitat, even though no endangered bats have been found there.

NOTE: In 1996, after this paper was written, 2 entrances at a new mine site (778) in Pike County were trapped a total of three times. A total of 88 bats was taken—44 little brown myotis, 25 eastern pipistrelles, 17 northern myotis, and 2 Indiana myotis. The latter two bats are the first individuals of an endangered species taken during this program. Both were males captured on 10 October 1996. This site will be investigated further.

ACKNOWLEDGMENTS

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